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Cover illustration: The earliest known photograph of a hunting bolas spider, *Mastophora bisaccata* (Family Araneidae). This remarkable photograph, circa 1953, is one of many taken by artist and self-taught arachnological hobbyist M. W. Tyler of Umatilla, Florida.

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GENETIC VARIABILITY AND GENE FLOW IN *METEPEIRA VENTURA* (ARANEAE, ARANEIDAE)

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ABSTRACT. Levels of genetic variability and gene flow among three populations of *Metepeira ventura* on Santa Catalina Island, California, were evaluated based on variation at 10 gene loci. Mean heterozygosity (observed) per population was 10.4% and mean polymorphism was 36.7%, consistent with levels of variability in other arthropods. Values of F_{ST} for the five polymorphic loci (mean F_{ST} = 0.009) suggest that gene flow prevents the genetic differentiation of these populations. The average number of migrants per generation (Nm) among these populations is estimated to be 28.6. The lack of inter-population genetic differentiation may result from aerial dispersal and/or crawling along vegetation by *M. ventura*. Such similarity may also be due to the more widespread vegetative cover of Santa Catalina prior to overgrazing, which may have physically united these populations in the recent past, allowing for gene flow among them.

Levi (1973) observed that, in general, smaller spiders have a greater number of species than larger forms. For example, the orb weaver genus *Araneus* in North America has about 20 species in the large-sized *diadematus* group, but over 30 small species (Levi 1971). Levi (1973) suggested that such a pattern might be due to discontinuities in the distribution of small species, permitting geographic speciation, as well as minimal genetic exchange among populations, perhaps related to habitat specialization. While small spiders might be expected to be easily dispersed among populations via ballooning (aerial transport on wind blown silk threads), it appears that ballooning is mainly a means of short-range movement *within* populations (Decae 1987).

The small orb weaver *Metepeira* is found throughout the Americas, including the California Channel Islands (Levi 1977). This spider spins an orb-web in low vegetation with an adjacent barrier web slightly to the side and above. The preferred web site is typically unobstructed, rigid vegetation, such as dead or leafless branches, cactus, signposts or fences (Levi 1977; Uetz & Burgess 1979). Individual *Metepeira* are generally solitary, though members of some species (e. g., *M. datona*, *M. spinipes*) are social (Schoener & Toft 1983; Uetz 1986, 1988). *Metepeira* have an annual life-cycle; spiderlings are born in spring and adults may be collected from summer to early fall (Levi 1977; Spiller 1984). Although other araneid spiderlings commonly balloon (Dean & Sterling 1985; Greenstone et al. 1987), this behavior has not been observed for *Metepeira* (Comstock 1948; Kaston 1948; Levi 1977).

On Santa Catalina Island, California, web sites of *M. ventura* appear to be preferentially located on the prickly-pear cacti *Opuntia littoralis* and *Opuntia oricola* (pers. obs.). *O. littoralis* and *O. oricola* are low, weedy cacti found in discontinuous patches on most parts of the island (Minnich 1980; M. Gay pers. comm.). Their presence appears to be positively correlated with the actions of feral herbivores (goats, pigs, sheep), whose rooting or browsing activities commonly eliminate or reduce most herbivorous vegetation (e. g., Brown 1980; Bennett 1993; Perlmutter 1993) but not the spiny *Opuntia* (Hobbs 1980; Minnich 1980). Given the mosaic distribution of *O. littoralis* and *O. oricola* on Santa Catalina, populations of *M. ventura* appear to be distributed in numerous, spatially isolated patches. In this study, we analyze patterns of genetic variation within and among *M. ventura* populations occupying such patches, as well as estimate levels of inter-population gene flow.

METHODS

Collections.—We collected *Metepeira* from three sites on Santa Catalina Island. The first site

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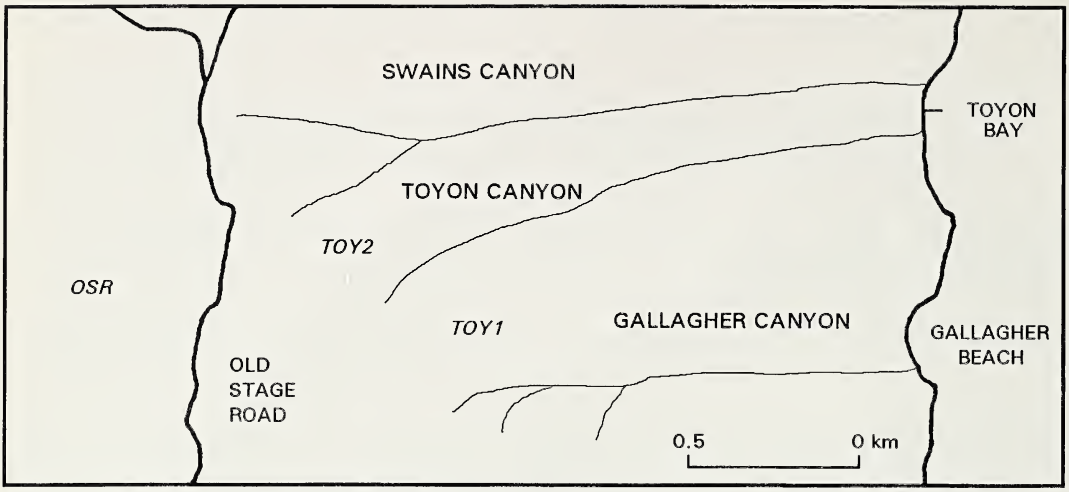

Figure 1.—Toyon Canyon region of Santa Catalina Island, California, showing *Metepeira ventura* sample sites. Population abbreviations follow Table 1.

(TOY1) was a 123 × 31 m area on a ridge between Gallagher Canyon and Toyon Canyon; the second site (TOY2) was a 92 × 31 m area on a ridge between Toyon Canyon and Swains Canyon, parallel to and north-west of the first site; and the third site (OSR) was a 80 × 31 m area west of the first two sites along Old Stage Road (Fig. 1). The vegetation at all sites primarily consisted of many small patches of *Opuntia*, intermixed with the bush *Rhus*, and all sites were bordered by more obstructed and/or less rigid vegetation (e. g., grasses), where *Metepeira* could seldom be found. Spiders were collected from *Opuntia* and from intermixed vegetation at the three sites. Sampling areas were not uniform because of the varying shapes and sizes of the vegetative patches at each site. Sample sizes were 42–43 spiders from each population (Table 1). In the laboratory, spiders were starved for at least a week and then frozen at −75 °C until they were prepared for electrophoresis.

Table 1.—Summary of collections of *Metepeira ventura* on Santa Catalina Island, California. Samples include spiders of all instars.

Locality (abbreviation)	Sample size	Dates of sampling
Toyon Canyon, S ridge (TOY1)	43	30 January, 1993
Toyon Canyon, N ridge (TOY2)	42	31 January, 1993
Old Stage Road (OSR)	43	6 February, 1993

Of the 11 species of *Metepeira* in California, four are known from the California Channel Islands: *M. crassipes*, *M. foxi*, *M. grinnelli* and *M. ventura* (Levi 1977). To ensure that we had pure samples, 68 adult male and female specimens collected at the three sites were examined by W. Icenogle and H. Levi and identified as *M. ventura*. Since the female epigynum and male palpus of juvenile *Metepeira* are undeveloped, immatures of this genus cannot be as readily identified to species (Levi 1977). To solve this problem, all spiders collected were examined under a Wild M3 microscope for the presence/absence of a white stripe on the sternum. A black sternum with no longitudinal stripe is a characteristic of *M. foxi* but not of *M. crassipes*, *M. grinnelli* or *M. ventura* (Levi 1977). All spiders collected had white stripes on their sternums, ruling out the presence of *M. foxi* in our samples. The stripes of very young juveniles and sub-adult males tended to be less distinct and appeared off-white in some individuals. The identification numbers of these spiders were recorded along with remarks about their appearance. This precaution was taken to determine later whether these individuals might exhibit unusual electrophoretic banding patterns, perhaps indicating their assignment to *M. crassipes* or *M. grinnelli*. No such electrophoretic differences were found, so we are confident our samples were pure *M. ventura*.

Electrophoresis.—A survey of 19 enzymes on up to two buffer systems (Appendix 1) revealed

Table 2.—Enzyme/buffer combinations for starch gel electrophoresis. E.C. number denotes Enzyme Commission identification number (Commission on Biochemical Nomenclature 1979). Buffer abbreviations follow Appendix 1.

Enzyme	# Loci	Abbrev.	E.C. number	Buffer
Adenylate kinase	1	ADKIN	2.7.4.3	TMA
Arginine phosphokinase	2	APK	2.7.3.3	REG
Fumarase	1	FUM	4.2.1.2	TMA
Glucosephosphate isomerase	1	GPI	5.3.1.9	REG
Glyceraldehyde-3-phosphate dehydrogenase	1	G-3-PDH	1.2.1.12	TC1
Isocitrate dehydrogenase	1	IDH	1.1.1.42	TMA
Phosphoglucomutase	2	PGM	2.7.5.1	TC1
Superoxide dismutase	1	SOD	1.15.1.1	REG

consistently scorable activity for 10 loci (Table 2); electrophoretic techniques and staining protocols are described in Ramirez (1990). Gels were 12.5% hydrolyzed starch (StarchArt Corporation). No significant differences in the banding patterns of spiders of different age or sex were ever detected, making it possible to examine spiders of all instars. All genotypes were inferred from the appearance of the staining patterns and the known subunit structure of the enzymes (Harris & Hopkinson 1976; Richardson et al. 1986).

Data analysis.—We used the BIOSYS-1 (version 1.7; Swofford & Selander 1981, 1989) computer package to analyze the electrophoretic data. Agreement between observed population genotypic ratios and Hardy-Weinberg expectations was evaluated by Chi-square tests for goodness of fit (Sokal & Rohlf 1981); Levene's (1949) correction for small sample size was applied to the expected frequencies. To test the null hypothesis that allele frequencies in the three populations are not significantly different, contingency table Chi-square analysis (Brower & Zar 1984) was performed. To determine the extent of heterozygote deficiency or excess in a population, Wright's (1969) fixation index was calculated for all polymorphic loci.

The apportionment of genetic differentiation among populations was analyzed by use of Wright's (1965) F_{ST} statistic as modified by Nei (1977). All F_{ST} values were calculated using means and variances of allele frequencies weighted by sample sizes. Gene flow (Nm) was estimated from the F_{ST} values, using the equation $Nm = (1 - F_{ST})/4F_{ST}$ (Wright 1951). The mathematical definitions of the population genetic parameters reported here can be found in standard population genetics textbooks (e. g., Hedrick 1985; Hartl & Clark 1989).

Table 3.—Allele frequencies in populations of *Metepeira ventura*. Population abbreviations follow Table 1, locus abbreviations follow Table 2, and sample sizes are in parentheses.

	Population		
Locus/allele	TOY1	TOY2	OSR
ADKIN	(43)	(42)	(41)
A	1.000	0.988	1.000
B	0.000	0.012	0.000
APK-1	(43)	(42)	(43)
A	1.000	1.000	1.000
APK-2	(43)	(42)	(43)
A	1.000	1.000	1.000
FUM	(43)	(42)	(43)
A	1.000	1.000	0.977
B	0.000	0.000	0.023
GPI	(43)	(42)	(43)
A	0.035	0.036	0.035
B	0.105	0.036	0.035
C	0.791	0.869	0.849
D	0.058	0.024	0.058
E	0.012	0.036	0.023
G-3-PDH	(43)	(42)	(43)
A	1.000	1.000	1.000
IDH	(43)	(42)	(43)
A	0.000	0.012	0.000
B	0.930	0.964	0.953
C	0.070	0.024	0.047
PGM-1	(43)	(42)	(41)
A	0.523	0.488	0.549
B	0.140	0.155	0.232
C	0.302	0.345	0.207
D	0.035	0.012	0.012
PGM-2	(43)	(42)	(41)
A	1.000	1.000	1.000
SOD	(43)	(42)	(43)
A	1.000	1.000	1.000

Table 4.—Genetic variability measures for the three study populations (± SE). n = mean sample size per locus; A = mean number of alleles per locus; P = % of loci polymorphic (a locus is considered polymorphic if the frequency of the most common allele does not exceed 0.99); H_o = observed heterozygosity; H_e = expected mean heterozygosity calculated using the unbiased estimate of Nei (1978). Population abbreviations follow Table 1.

Population	n	A	P	H_o	H_e
TOY1	43.0	1.8 ± 0.5	30.0	0.109 ± 0.064	0.112 ± 0.068
TOY2	42.0	2.0 ± 0.5	40.0	0.095 ± 0.063	0.096 ± 0.064
OSR	42.4	1.9 ± 0.5	40.0	0.108 ± 0.071	0.102 ± 0.063

RESULTS

There were 21 alleles identified at the 10 genetic loci (Table 3); five loci (APK-1, APK-2, G-3-PDH, PGM-2, SOD) were monomorphic across all three populations. The five remaining loci (ADKIN, FUM, GPI, IDH, PGM-l) were polymorphic for two or more alleles in at least one of the three sites. Alleles unique to particular sites (private alleles) were nonexistent (TOY1) or rare (OSR, TOY2) (Table 3).

Population variability.—In general, the variability of individual *Metepeira* populations was high (Table 4). The mean number of alleles per locus was 1.9 (range = 1.8–2.0), mean heterozygosity (observed) was 0.104 (range = 0.095–0.109), and mean polymorphism was 36.7% (range = 30.0–40.0%).

Gene frequencies in population subsamples deviated significantly from Hardy-Weinberg expectations in only one of the 11 cases with polymorphic loci (Table 5). Values of Wright's (1969) fixation index for each polymorphic locus ranged from −0.134 to +1.00 (Table 5), with the largest positive value (1.00; indicative of heterozygote deficiency) being found for the single case (FUM) which deviated significantly from Hardy-Weinberg equilibrium. Thus, individual populations were essentially in conformance with Hardy-Weinberg equilibrium and in the one case where significant deviation was indicated, it was in the form of heterozygote deficiency.

Interpopulation differentiation and gene flow.—Allele frequencies for polymorphic loci were not significantly different among the three populations (Table 6). Populations were also minimally structured as indicated by Wright's F_{ST} statistic (Wright 1965; Nei 1977) (Table 7). On average, approximately 0.9% of the total variance in allele frequencies in *M. ventura* was due to genetic differences among populations, with the remainder of the total gene diversity (99.1%) being found among spiders within any given population ($1 - F_{ST}$). Using the F_{ST} values to estimate gene flow, the mean number of migrants per generation (Nm) among these populations is 28.6 (Table 7). This value, as well as all Nm values in Table 7, are well above the theoretical threshold level at which gene flow is sufficient to homogenize populations genetically in the absence of selection (Nm = 1; Slatkin 1987). Hence, these spatially separate populations are statistically part of a single, minimally-structured unit with an undifferentiated gene pool, presumably maintained by significant gene flow.

DISCUSSION

Population variability.—*Metepeira ventura* populations on Santa Catalina Island are highly variable and in Hardy-Weinberg equilibrium. In their review of allozyme variation, Nevo et al. (1984) reported the following values of mean observed heterozygosity (H_o) and polymorphism

Table 5.—Fixation index values for each polymorphic locus in each population. Missing values indicate a locus not polymorhpic in that population. Significance levels indicate the results of Chi-square tests for deviation from Hardy-Weinberg equilibrium at polymorphic loci in each population. Population abbreviations follow Table 1. * $P < 0.001$.

	Locus				
Population	ADKIN	FUM	GPI	IDH	PGM-1
TOY1	—	—	−0.101	−0.075	0.091
TOY2	−0.012	—	0.009	−0.029	−0.001
OSR	—	1.00*	−0.107	−0.049	−0.134

Table 6.—Results of contingency Chi-square analysis of polymorphic loci. The null hypothesis is that there is no significant variation in allele frequencies among populations. Locus abbreviations follow Table 2.

Locus	Number of alleles	χ^2	df	*P*
ADKIN	2	2.008	2	0.36642
FUM	2	3.985	2	0.13638
GPI	5	7.499	8	0.48387
IDH	3	4.017	4	0.40369
PGM-1	4	7.001	6	0.32074
	(Totals)	24.510	22	0.32108

Table 7.—Values of F_{ST} and Nm for each variable locus. The F_{ST} values are the averages for a locus of the values computed for each allele. The estimates of Nm are based on Wright's (1951) formula: $Nm = (1 - F_{ST})/4F_{ST}$. Locus abbreviations follow Table 2.

Locus	F_{ST}	Nm
ADKIN	0.008	31.0
FUM	0.016	15.4
GPI	0.009	27.5
IDH	0.006	41.4
PGM-1	0.009	27.5
Mean	0.009	28.6

(P, % of loci polymorphic) for invertebrates: invertebrates in general, $H_o = 10.0\%$ and $P = 37.5\%$; *Drosophila* species, $H_o = 12.3\%$, $P = 48.0\%$; other insects, $H_o = 8.9\%$, $P = 35.1\%$; and chelicerates (including spiders), $H_o = 8.0\%$, $P = 26.9\%$. Among spiders, variability levels have been reported for three araneids: *Araneus ventricosus* ($H_o = 9.4$, $P = 20.0\%$) (Manchenko 1981); *Meta menardi* ($H_o = 2.7\%$, $P = 9.6\%$) (Laing et al. 1976); and *Metepeira spinipes* ($H_o = 17.2\%$, P not reported) (Uetz et al. 1986). The lower values for *Meta menardi* may be related to its cave-dwelling existence (Culver 1982). Thus, levels of variability in *M. ventura* ($H_o = 10.4\%$, $P = 36.7\%$) are consistent with those for invertebrates and other araneids (save for *Meta menardi*).

Gene flow.—The patchy distribution of *Opuntia* on Santa Catalina Island organizes *M. ventura* into numerous local populations. The low values of F_{ST} and large values of Nm indicate that gene flow is sufficiently strong that it prevents genetic drift from causing local genetic differentiation. Clearly, Levi's (1973) suggestion that populations of small spider species experience minimal genetic exchange does not apply to these populations of *M. ventura*. However, these populations are fairly close together and a study of more widely spaced samples may show that gene flow drops off considerably beyond a particular interpopulation distance, consistent with Levi's hypothesis.

Since Nm estimates derived from allele frequency data may be due to both *contemporary* and *historic* opportunities for gene flow (Slatkin 1987), it is important to consider such possibilities for *M. ventura*. While no *Metepeira* have been reported to balloon, little is known of the biology of many species (Levi 1977) and so it is possible that *M. ventura* may be capable of aerial dispersal. If so, interpopulation movement could be via ballooning and/or crawling along vegetation. Uetz et al. (1982) marked adults and juveniles of the social *M. spinipes* from various local colonies in central Mexico and noted little change during several months in colony membership. While this study would seem to indicate that *Metepeira* have limited dispersal tendencies, it may be unwise to generalize from the social *M. spinipes* to solitary species like *M. ventura*, since sociality may select for colony fidelity (Uetz et al. 1982; Uetz 1986). On the other hand, Uetz et al. (1982) also found that optimal web sites for *M. spinipes* were in *Agave* and *Opuntia* and since such cacti were patchily distributed in their study area, they suggested that selection might favor individuals which stayed in their respective patches. While the same reasoning would seem to hold for *M. ventura* and *Opuntia* on Santa Catalina, only a long-term study of the movements of marked individuals can determine contemporary levels of migration and, thus, of gene flow.

Historically, interpopulation gene flow would presumably have been facilitated by the more widespread vegetative cover of Santa Catalina prior to human-caused alterations. The island has been severely overgrazed for over a century by introduced bison, deer, goats, pigs and other livestock, significantly reducing the amount of chaparral and coastal sage scrub habitat (Minnich 1980). This enabled the normally coastal *Opuntia littoralis* and *O. oricola* to spread into bare inland areas (Sauer 1988; M. Gay pers. comm.). In contrast, near the city of Avalon and other areas of decreased grazing, contiguous stands of native vegetation are extensive (cover can exceed 70%) (Coblentz 1980; Minnich 1980). Thus, the high Nm value for *M. ventura* is likely

due at least in part to the less open landscape of pre-human Santa Catalina. In the future, we plan to use both direct (marking) and indirect (genetic) means to determine movement among web sites at varying inter-population distances in both heavily grazed and more natural areas to clarify the exact relationship between distance, the vegetative matrix and gene flow in *M. ventura*.

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Appendix 1.—List of enzymes screened, standard abbreviations and buffer systems with which enzymatic activity was assayed in *Metepeira ventura.* X = good results; 0 = no activity or poor results. Buffer abbreviations: REG—Discontinuous Tris-citrate (Poulik 1957); TC1—Continuous Tris-citrate I (Selander et al. 1971); TMA—Tris-maleate (Selander et al. 1971).

		Buffer		
Enzyme	Abbrev.	REG	TC1	TMA
Adenylate kinase	ADKIN			X
Alcohol dehydrogenase	ADH	0		
Arginine phosphokinase	APK	X		
Asparate aminotransferase	AAT		0	
Fumarase	FUM			X
Glucosephosphate isomerase	GPI	X	0	
Glyceraldehyde-3-phosphate dehydrogenase	G-3-PDH		X	
α-Glycerophosphate dehydrogenase	α-GPDH		0	
Hexokinase	HK	0		
Isocitrate dehydrogenase	IDH			X
Lactate dehydrogenase	LDH	0		
Malate dehydrogenase	MDH			0
Malic enzyme	ME			0
Nucleoside phosphorylase	NP			0
Peptidase with leucyl-alanine	PEP(LA)	0		
Phosphoglucomutase	PGM	0	X	
Phosphomannose isomerase	PMI			0
Superoxide dismutase	SOD	X		
Triosephosphate isomerase	TPI			0

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VOLATILE CHEMICAL CUE ELICITS MATING BEHAVIOR OF COHABITING MALES OF *NEPHILA CLAVATA* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. Previous studies have revealed that matings of the spider *Nephila clavata* are concentrated just after the final molt of females. We determined the existence of a chemical cue eliciting male mating behavior in this particular period by three experiments. First, an immobile spider anesthetized with CO_2 was placed in a web, and the behavioral response of an introduced male was observed. Males approached and exhibited mating behavior to newly-molted immobile spiders irrespective of the stage and sex, while these behaviors seldom occurred to immobile spiders that were more than 24 hours past molting. Secondly, an olfactometer experiment revealed that newly-molted females attracted males much more frequently than females more than 24 hours past molting. Thirdly, the acetone-soluble extract of the body surface of newly-molted females was absorbed on to a piece of filter paper, and it was placed near the female which had been killed. Males approached and touched the female having the extract more frequently than the female without it. These results indicate the existence of a volatile chemical cue emitted by newly-molted individuals which elicits mating behavior in cohabiting males. This cue may be a compound involved in the molting fluid and may not be a special substance designed for sexual communication.

Adult males of the orb web spiders in the genus *Nephila* cohabit with females on their webs, and they copulate just after the final molt of females or while the females are feeding on large prey (Robinson & Robinson 1973; Christenson et al. 1985; Miyashita 1993). In *N. clavata*, most matings occurred just after the final molt of the females (Miyashita 1993). Since this species shows no obvious courtship behavior (Yoshikura 1987) and females are much larger than males, females are dangerous partners for males. However, safe copulation should be ensured when males copulate with newly-molted females which have soft exoskeletons and are not aggressive toward males. Moreover, Christenson & Cohn (1988) have demonstrated that *N. clavipes* has first male sperm precedence. This enhances the importance of early copulation and may have driven the evolution of precopulatory guarding by males. Preliminary observations have indicated that a male introduced artificially onto the web of a newly-molted female will approach the female immediately and copulate. This suggests that a chemical substance emitted by newly-molted females may elicit mating behavior of cohabiting males.

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There have been many lines of evidence for the existence of sex-related chemical cues in spiders; some are air-borne (Blanke 1975; Tietjen 1979; Olive 1982; Watson 1986; Schulz & Toft 1993) and others are contact pheromones that are borne by web silk (Ross & Smith 1979; Tietjen & Rovner 1982; Suter & Renkes 1982; Jackson 1986; Suter & Hirscheimer 1986). However, there has been no evidence that volatile chemicals emitted by newly-molted females induce male mating behavior.

The aims of the present paper are to test for the existence of a chemical emitted by newly-molted females and to determine whether this substance is unique to newly-molted adult females.

METHODS

Reproductive biology of the spider.—*Nephila clavata* has one generation per year. After overwintering as eggs, spiderlings emerge in June in central Japan. Males begin to reach maturity from late August while females mature in September and early October. Adult females are much larger than adult males (females, 12–28 mm body length; males, 3–9 mm). Adult males do not construct their own webs but cohabit on the webs with females. When more than one male attends

a female, male-male combat is occasionally observed. The larger male usually occupies the hub position on the web and has the advantage in mating. More than 80% of copulations were observed just after the final molt of females (Miyashita 1993). Oviposition takes place from mid-October to November, and only one clutch is laid by a female.

Subjects and housing.—All individuals used in our experiments were collected from small woodlands in Tokyo and Yokohama City in Japan. Adult males were collected from female webs in late August and early September when no adult female was present. Each male was kept in a small plastic cup (*ca.* 10 cm × 4 cm) and was supplied with water by spraying every two days. All males in the experiments were used within two weeks following capture. Subadult males collected in September were reared individually in a cage that was 45 cm × 45cm × 45 cm. The top and the bottom of the cage were made of wooden plates, two sides were of fine mesh net, and the other two sides were sheet vinyl. A mealworm was supplied to each spider every 2–3 days. We reared spiders at room temperatures and under a natural light cycle.

Females that are near to molt are easily identified in the field by their characteristic abdominal coloration and by their reduced spiral threads. To obtain newly-molted individuals, females were collected in September and were housed as described above. Most females molted within a few days of collection. Females that were more than 24 hours past molting were collected from the field in September and early October, and the developmental stage (adult or subadult) was determined by inspecting the epigynum.

Responses to whole spiders.—In order to determine whether only newly-molted adult females elicit mating behavior of males, we examined the response of males to six groups of spiders: 1) newly-molted (1–3 hours after molting) subadult females (NSF), 2) subadult females more than 24 hours after molting (SF), 3) newly-molted adult females (NAF), 4) adult females more than 24 hours after molting (AF), 5) newly-molted adult males (NAM), and 6) adult males more than 24 hours after molting (AM).

The experimental procedure was as follows. First, we introduced a SF spider into the cage described above to obtain an intact web in the cage. After construction of the web, the spider was removed from the cage. Another spider that belonged to one of these six groups was anesthetized with CO_2 for about an hour. This immobile spider was placed gently at the center of the web with forceps. The spider hung head-up on the upper side of the inclined orb-web. Lastly, we introduced an adult male onto the lower part of the web (about 40 cm below the immobile spider), and the subsequent behavioral response of the male spider to the immobile spider was recorded. We recorded the following five behavioral traits of the male. 1) "orientation": the male spider walked toward the immobile spider and the distance between them was less than 3 cm; 2) "contact with legs"; 3) "contact with palps": the male spider touched the cephalothorax or abdomen of the immobile spider by palps; 4) "repeated contact": the male spider continued "contact with legs" for 10 minutes or it repeated "contact with palps" three times. Actual copulations were not observed, probably due to the unnatural posture and/or anesthetization of the immobile spider. Each experiment was terminated when either of the following three conditions occurred: 1) the male spider went out of the web, 2) "repeated contact" was recorded, or 3) the male spider remained motionless for 30 min. This experiment was conducted under windless conditions.

Olfactometer.—We used an olfactometer for examining whether male spiders approach females by means of air-borne substance (Fig. 1). Wire-net was attached to the inner side of the walk tunnel so that male spiders could walk easily. The female box and the walk tunnel were separated by a double fine-mesh wire-net, which made the female invisible to the male. The air current in the olfactometer was created by a fan attached to the ventilation. The wind speed was set at 11 cm/sec, which did not seem to prevent spiders from walking upwind. We first introduced a female into the female box (either NSF, SF, NAF, or AF). Next, a male was introduced into the entrance of the walk tunnel. Two hours later, we checked the location of the male, and if it was located within 15 cm from the double wire-net separating the female box and the walk tunnel, it was regarded as a positive response. At the end of each experiment, the olfactometer was washed with acetone. Experiments with no individuals in the female box were conducted as controls.

Responses to extracts.—We examined whether an extract of the body surface of newly-molted females elicited mating behavior in males. The experimental procedure was as follows. (1) Sub-

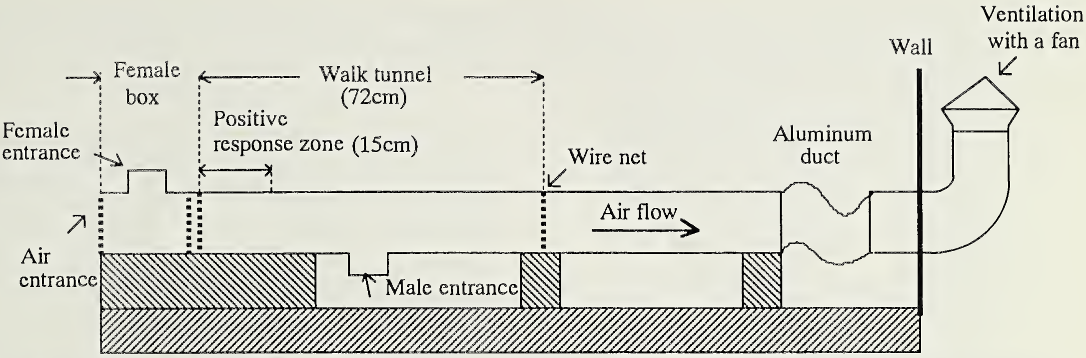

Figure 1.—The olfactormeter used in Experiment II. "Walk tunnel" is made of a transparent acrylic pipe.

adult females that were more than 24 hours past molting were killed in a refrigerator, to be used as "dummy females". (2) A total of 12 newly-molted adult females was killed with CO_2 and then soaked in 15 ml of acetone for five minutes. This fluid may contain chemical substances derived from the body surface as well as from the internal organs, and is called the extract. Since the fluid remained clear after spiders were soaked, it probably contained little material from the internal organs. (3) An adult female, more than 24 hours after molting, was released into the cage and then removed after completion of the web. (4) A "dummy female" was placed at the center of the web as the same manner as in Experiment I. (5) We let fall a few drops of extract (concentration: about 0.2 female equivalent) or acetone (control) on a small piece of a filter paper (1 cm × 1 cm) and dried the paper in air for a few minutes. It was then carefully placed on the web three cm below the "dummy female". (6) Finally, an adult male was introduced onto the web and subsequent behaviors were recorded as in Experiment I. The experiment was conducted under windless conditions.

RESULTS

Responses to whole spiders.—Responses of males were greater to newly-molted individuals than to those more than 24 hours past molting. This relationship was observed consistently for subadult females, adult females, and even adult males (Table 1). The behavioral traits most characteristic of mating were "contact with palps" and "repeated contact"; and these two behaviors were seldom performed toward individuals that were more than 24 hours past molting, irrespective of the stage and sex. On the other hand, nearly half of the males touched the newly-molted individuals with their palps and showed "repeated contact" (Table 1).

For newly-molted individuals, there were no significant differences between subadult and adult females in all behavioral traits of males (Table 1); and, also, there were no differences in male responses to adult males and females (Table 1). Similarly, for individuals more than 24 hours past molting, there were also no significant differences between ages nor between sexes. These results strongly suggest that newly-molted individuals, irrespective of the stage and sex, produce the stimulus attracting and causing mating behavior in males.

Olfactometer.—In the control experiment in which no female was present in the "female box", 17% of males were located in the area of "positive response" (Table 2). This may be regarded as the result of random walking within the tunnel. Significantly larger percentages of males exposed to newly-molted females were located in the positive response area than those in the control (Table 2). On the other hand, no differences were found in the frequencies of males showing positive response between the control and those exposed to females more than 24 hours past molting (Table 2). These results are consistent with those of the experiment with whole spiders and show that an air-borne substance emitted by newly-molted females attracted the males.

Responses to extracts.—All males showed "orientation" and 90% of them exhibited "contact with legs" to "dummy females" with extract, while 20% of males showed the above behaviors to the females with acetone (control, Table 3). Thus, body surface extract of newly-molted females attracted males. However, there were no differences between the controls and the females with extract in the frequences of males showing

Table 1.—Number of *Nephila clavata* males that exhibited each behavioral response to anesthetized immobile conspecific spiders on webs in Experiment I. Values in parentheses represent percentages of the total numbers. Differences in frequencies between immobile spiders were tested by Fisher's exact probability test. Asterisks attached to probabilities indicate that these probabilities are significant at 5% level of adjusted significance ($\alpha = 0.0073$; Dunn-Sidák method) with seven pairwise comparisons. NSF: newly molted subadult female, SF: subadult female, NAF: newly molted adult female, AF: adult female, NAM: newly molted adult male, AM: adult male.

Male behavior	NSF +	NSF −	SF +	SF −	NSF vs. SF (*P*)	NAF +	NAF −	AF +	AF −	NAF vs. AF (*P*)	NAM +	NAM −	AM +	AM −	NAM vs. AM (*P*)	NSF vs. NAF (*P*)	NAF vs. NAM (*P*)	SF vs. AF (*P*)	AF vs. AM (*P*)
Orientation	9 (90)	1 (10)	7 (23)	23 (77)	<0.001*	17 (71)	7 (29)	5 (25)	15 (75)	0.003*	5 (71)	2 (29)	6 (21)	22 (79)	0.021	0.231	0.681	0.685	0.740
Contact with legs	9 (90)	1 (10)	4 (13)	26 (87)	<0.001*	14 (58)	10 (42)	4 (20)	16 (80)	0.011	5 (71)	2 (29)	4 (14)	24 (86)	0.006*	0.077	0.435	0.401	0.442
Contact with palps	6 (60)	4 (40)	1 (3)	29 (97)	<0.001*	11 (46)	13 (54)	0 (0)	20 (100)	<0.001*	4 (57)	3 (43)	2 (7)	26 (93)	0.009	0.354	0.461	0.600	0.335
Repeated contact	6 (60)	4 (40)	0 (0)	30 (100)	<0.001*	11 (46)	13 (54)	0 (0)	20 (100)	<0.001*	3 (43)	4 (57)	1 (4)	27 (96)	0.019	0.354	0.617	1.000	0.583

"contact with palps" and "repeated contact" to the females (Table 3).

DISCUSSION

Evidence of a volatile chemical cue.—Male spiders approached newly-molted individuals and exhibited mating behavior such as touching them with palps, but they rarely showed such responses to individuals that were more than 24 hours past molting (Table 1). The webs used in the whole spider experiment were all derived from subadult females that were more than 24 hours past molting. Moreover, anesthetized immobile spiders could not add silk to the webs. Therefore, it seems that a volatile substance from the body, and not from the silk, elicited orientation and mating behavior of males. This was strongly supported by the olfactometer experiment in which males were attracted upwind toward newly-molted, invisible females (Table 2).

The frequencies of males trying "contact with palps" and "repeated contact" were not very high (about 50%) in the experiment with whole spiders. This could be due to the unnatural posture of the immobile spider, which hung head-up on the upper side of the inclined orb-web. Alternatively, immobilization of spiders by CO_2 itself may prevent normal mating behavior of males. In the olfactometer experiment, the percentage of males that approached newly-molted females was 60% (Table 2). This may indicate that the attractiveness of this volatile substance is not

Table 2.—Number of *Nephila clavata* males located at the positive response zone within the olfactometer in Experiment II. Values in parentheses are percentages of total males. Differences in frequencies between treatments and a control were tested by Fisher's exact probability test. Asterisks attached to probabilities indicate that these probabilities are significant at 5% level of adjusted significance ($\alpha = 0.013$; Dunn-Sidák method) with four pairwise comparisons. NSF: newly molted subadult female, SF: subadult female, NAF: newly molted adult female, AF: adult female, control: no spider.

Spiders tested	Response +	Response −	Comparison with control (*P*)
NSF	6 (60)	4 (40)	0.019
SF	2 (11)	16 (89)	0.481
NAF	15 (60)	10 (40)	0.002*
AF	3 (17)	15 (83)	0.665
Control	4 (17)	20 (83)	

Table 3.—Number of *Nephila clavata* males exhibiting each behavioral response to dummy females with or without extract of the body surface of newly molted adult females *N. clavata* (Experiment III).

Male behavior	With extract +	With extract −	Without extract +	Without extract −	Fisher's test *P*
Orientation	10 (100)	0 (0)	2 (20)	8 (80)	<0.001
Contact with legs	9 (90)	1 (10)	2 (20)	8 (80)	<0.001
Contact with palps	1 (10)	9 (90)	0 (0)	10 (100)	0.500
Repeated contact	1 (10)	9 (90)	0 (0)	10 (100)	0.500

very strong over long distances. Nevertheless, to attract and cause mating behavior of males cohabiting in the same web, this substance should be effective because the distance between the two sexes in nature is, at most, about 30 cm (pers. obs.). Other mechanisms must be used by males to locate female webs.

The experiment with extracts revealed that a chemical substance present on the body surface of newly-molted females attracts males (Table 3). However, males rarely touched the dummy female with their palps, which is a characteristic mating behavior. This is probably because extract from the female body surface is on the small filter paper placed near the dummy female, not on the body of the dummy female. Although males are attracted to females by the volatile substance and touched the body with their legs, subsequent mating behavior may require chemical stimulus that is detected when the legs contact the body surface of newly-molted females.

Characteristics of the chemical cue.—The chemical cue found here is an air-borne substance emitted by newly-molted individuals which causes mating behavior of cohabiting males. It is especially noteworthy that not only do adult females produce this cue but subadult and even adult males do, also.

There have been several reports on the existence of air-borne sex-related chemical cues in spiders (Blanke 1975; Tietjen 1979; Olive 1982; Watson 1986; Schulz & Toft 1993). All of these spiders use chemical cues to attract males from outside their webs, but they do not appear to use it to elicit mating behavior of cohabiting males. Chemical cues causing orientation and courtship behavior of cohabiting males (i.e., within the web) are known in some spiders (Ross & Smith 1979; Suter & Renkes 1982; Suter & Hirscheimer 1986), but all of these are contact cues contained in the web silk. Thus, the sex-related chemical cue of *N. clavata* has a unique characteristic: although it is air-borne, it elicits mating behavior of cohabiting males, which is functionally similar to the contact cues mentioned above. To our knowledge, this type of chemical cue has not been published previously.

Another important feature of this cue is that it is emitted just after the molt. In a jumping spider *Phidippus johnsoni*, the contact pheromone that arrests males near the immature female is contained in the web silk of females which are about to molt (Jackson 1986). However, this functions to make males cohabit with females, not to stimulate mating behavior. In other Arthropoda, there are a few examples of sex pheromones which are emitted at or near the time of the molt: males of some crab species exhibited a typical display behavior when exposed to the water from a tank containing a premolt female crab (Ryan 1966; Kittredge & Takahashi 1972); and males of some butterflies gather around pupae that are about to eclose (Brown 1981; Elgar & Pierce 1988). Elgar & Pierce (1988) have suggested that a volatile substance emitted by late-stage pupae attracts males of the Lycaenid butterfly, *Jalmenus evagoras*, because if an observer crushes a late-stage pupa, the person's fingers also become attractive to males. Interestingly, this butterfly cannot detect the difference between male and female pupae, which is similar to *N. clavata* because males exhibited mating behavior to both newly-molted males and newly-molted females. Therefore, the chemical cue of *N. clavata* seems to have an origin similar to that in the crabs and the butterfly described above: all of them must be derived from some compounds related to molting. The chemical cue of this spider may be a compound involved in the molting fluid, and is probably not a substance specially designed for sexual communication because it is hard to imagine that males and juveniles developed a special machinery with no benefit to them. In this context, the cue found in

the present study is neither a communicating substance nor a sex pheromone in the strict sense (Krebs & Davies 1993; Williams 1992).

Significance of the chemical cue.—In spiders, males are usually smaller than females. This is especially true for *N. clavata* in which male body length is ½–⅓ of female body length (Miyashita 1993). Moreover, males of this species show no obvious courtship behavior to females (Yoshikura 1987), unlike many other orb-weavers (Robinson & Robinson 1980). Thus, the predatory nature of the spider makes females potentially dangerous for males. Just after the final molt of a female, however, a male is able to copulate without the danger of being eaten by a large partner because she is not aggressive due to her soft exoskeleton. Furthermore, selection must have favored early copulation since first male sperm precedence is known in a congener *N. clavipes* (Christenson & Cohn 1988). Thus, the adaptive significance of males using an odor emitted by just molted females is obvious.

Since males approached and exhibited mating behavior to males and subadult females which had just molted, one may consider the disadvantage of using such a non-specific cue. Despite intensive field observations conducted for three years, no adult males were found to cohabit on subadult male webs (Miyashita pers. obs.). Thus, attempting to mate with a newly-molted male is unlikely in nature because the chemical cue seems to be effective only within the web. We observed two instances in which a male was trying to copulate with a newly-molted subadult female. Also, Christenson et al. (1985) reported two examples of juvenile copulation in *N. clavipes*. This seems rather exceptional in nature, however, because the probability of an adult male cohabiting with a female of a pre-subadult stage is low. Therefore, the disadvantages of using a non-sex-specific and non-stage-specific cue appears to be small, and hence selection has favored males that responded to a chemical cue without a sexual function that was produced by newly-molted individuals. A similar view of the origin of some sex pheromones was proposed by Kittredge & Takahashi (1972) and Thornhill (1979).

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CONSPECIFIC INTERACTIONS IN THE LYCOSID SPIDER *RABIDOSA RABIDA*: THE ROLES OF DIFFERENT SENSES

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ABSTRACT. The behavior of sighted and of blind male and female *Rabidosa rabida* paired in various combinations was videotaped and analyzed. When walking, neither sighted nor blind spiders could detect motionless conspecifics prior to contact. When motionless, blind males detected moving females at greater distances than they detected moving males. However, neither sighted nor blind motionless males detected very slowly moving females at any distance. These data suggested for *R. rabida*: (1) the effectiveness of visually and vibrationally cryptic locomotion, (2) a lack of form vision, and (3) absence of a close-range, air-borne pheromone. In both sexes, visual detection of moving conspecifics by motionless spiders provided for accurate orientation responses at greater distances than did mechanoreception. Nonetheless, blind females could orient accurately toward courting males at close range based on vibrations. Blind males showed courtship display when briefly contacted by another male, suggesting an inadequate chemically based sex-recognition mechanism. Sighted males showed courtship display after visually detecting a walking male, but did not do so in response to a courting male, i.e., mutual courtship did not occur. Blind males sometimes did perform mutual courtship, suggesting an inadequate vibratory recognition mechanism. Unlike salticids, these lycosids did not require vision to initiate either agonistic display or ritualized fighting.

To the human observer, wolf spiders usually appear to be responding to one another on the basis of visual information. Indeed, the use of video image presentation in studies of certain species of *Schizocosa* Chamberlin 1904 by McClintock & Uetz (in press) and E. Hebets & G. Uetz (unpubl.) have demonstrated that some lycosid spiders can rely primarily on visual cues to mediate intraspecific interactions. The roles of different pairs of eyes in such responsiveness by the lycosid spider *Rabidosa rabida* (Walckenaer 1837) also have been elucidated by video playback (Rovner 1993).

Nonetheless, under natural conditions, when two spiders located close to each other share the same substratum, the possibility that mechanoreception plays the predominant role must be kept in mind. In related work, the latter was shown to be the case for interspecific interactions involving wolf spiders (*Rabidosa rabida*) that prey on fireflies (*Photuris* spp.) (Lizotte & Rovner 1988), for which it had previously been assumed that such predation was primarily visually based. The extreme sensitivity of the spider's metatarsal lyriform organs (slit sensillae) and trichobothria, both of which detect vibrations, has been well documented (Barth 1985; Reissland & Görner 1985).

In the present study I sought to determine the relative importances of vision, mechanoreception, and chemoreception for mediating conspecific interactions in the lycosid spider *Rabidosa rabida*. To do this, I compared the behavior of sighted spiders to the behavior of blind ones. Both male-female and male-male encounters were included in this investigation.

I chose *R. rabida* for the present study because all three channels of communication have been demonstrated to be used by this species. The adult males (unlike immature males and females of all instars) possess black legs I and silvery-white palpal tarsi, both of which are waved in stereotyped patterns during courtship display (Kaston 1936; Rovner 1968). Video playback of this behavior revealed that the leg I extension component triggers each bout of the female's receptive display (Rovner 1993). On the other hand, in the male's courtship display, the inclusion of an acoustic signal, which by itself can trigger each bout of receptive display in females (Rovner 1967), plus the occurrence of mating and other behaviors during nighttime as well

as daytime (*ibid.*) indicate that vision should not be assumed to be the most important sense used by this species. In addition, one must consider the possible roles of chemical signals, since a contact sex pheromone present on the female's dragline is known to play an important role in the male's search for the female (Tietjen 1977).

METHODS

The species used in this study was the subject of numerous papers during the previous three decades that examined various aspects of communication, reproduction, and prey capture. In those papers the species name was given as *Lycosa rabida* Walckenaer. In the present study the name *Rabidosa rabida* (Walckenaer) is used, in light of the recent revision by Brady & McKinley (1994).

Penultimate *R. rabida* were collected in late June 1991, 1992, and 1993 in Athens County, Ohio, USA. Voucher specimens of the resulting adults have been deposited in The Field Museum, Chicago.

The methods of maintenance and the laboratory conditions during data collection have been described previously (Rovner 1989). Spiders were not paired for observation until one week after their final molt. Each individual was used once, so that none would be affected by the experience of a prior encounter with a conspecific. Observations were made at various times of the day between 1000 h and 2200 h.

To cover the eyes of spiders, I painted them with two coats of dark-colored, water-based enamel (Top Color Hobbylack, Pelikan AG). That this ensured complete occlusion had been established previously (*ibid.*). Spiders that had been blinded were used in data collection one or more days after undergoing the occlusion procedure.

For data collection, each pair of spiders was introduced into a glass-topped wooden cage (125 mm × 100 mm × 35 mm high; a fresh piece of paper substratum was placed on the floor of the arena for each trial). Several minutes elapsed between the introduction of the first and second spiders. Behavior was recorded on videotape (Sony SL-HFR70 videocassette recorder). The camera (JVC GX-8NU) was aimed at a front-silvered mirror that was located 0.5 m above the arena floor and which had been fixed at a 45° angle to the arena floor. This yielded a dorsal view of the spider, which facilitated the later measurements of distances between spiders and of turning angles (accurate to the nearest 5°). Substratum vibrations were recorded on the audio track by use of a vibration pickup system (General Radio 1560-P14) connected to a sound-level meter (General Radio 1551-C), whose output was fed into the video camera.

For male–female interactions, 10 males and 10 females were used in 10 trials for each of four types of pairings: sighted male–sighted female; blind male–sighted female; sighted male–blind female; and blind male–blind female. Thus, the behavior of 40 males and 40 females heterosexually paired was recorded and analyzed.

For male–male interactions, 20 males were used in 10 trials for each of three types of pairings: sighted male–sighted male; blind male–sighted male; and blind male–blind male. Thus, the behavior of 60 males encountering other males was recorded and analyzed.

I arbitrarily used the distance between the faces of the two spiders as the basis for measuring the distance between individuals. To help the reader visualize the distances, they are first roughly given as approximate body lengths, rounded to the nearest 0.5 body length (MBL = male body lengths; FBL = female body lengths) and then, more precisely, in mm. Males averaged 12 mm in length; females, 18 mm. (Because of the limited size of the arena, a size chosen to provide sufficiently detailed images of the spiders via the fixed video camera, the maximum possible distances over which some visual responses could be elicited were not determined. The reader will be reminded of this by my use of the phrase "at distances of up to at least. . .").

Because only the largest distances and turning angles observed were the data of interest with regard to assessing the relative effectiveness of the various signals and receptors involved in the spiders' interactions, only the maximum values are given in this paper for the various data sets. Another reason for not using mean values was that the distances and turning angles associated with interacting spiders were highly variable (non-normally distributed). This was because, unlike an experiment in which investigator-controlled stimuli are presented to a single test spider from one or two predetermined directions, the locations

Figure 1.—The stationary, sighted male *Rabidosa rabida* (at right) did not respond to the slowly wandering female as she approached, resulting in the overlap (but not contact) of the female's right leg II and the male's left leg IV. (In this and all other figures, the spiders are on the horizontal arena floor being viewed from above.)

and orientations of freely roaming spiders at the onset of a response by either of the spiders were unpredictable, as were the amplitudes of stimulating vibrations or movements produced by each member of the pair at any one moment.

One other category of data will be provided in this paper. For male-male interactions, the proportion of spiders (within each group of pairings) that showed a particular behavior is given parenthetically as a percentage (e.g., 13 of 20 males = 65%).

MALE–FEMALE INTERACTIONS

Stationary male approached by a female.—Both sighted and blind motionless males occasionally failed to respond to females that wandered very slowly toward them and got so close (2 MBL (26 mm) or nearer) as to have overlapping legs (Fig. 1). Usually, however, blind males turned toward a female approaching from any direction at a distance of up to 4 MBL (46 mm), as did sighted males at even greater distances.

Motionless males sometimes responded to an approaching female by a withdrawal response, either backing up a short distance or running away rapidly. These responses were triggered at distances of up to about 4.5 MBL (52 mm) in sighted males. If the male was courting, his typical response to a female that approached to within 3 MBL (37 mm), especially to a female performing a receptive display (Rovner 1967), was to suddenly "lean back" and to increase the flexure of legs I, thereby pulling himself into a "tightened" courtship posture. He subsequently also shortened the distance covered by his leg I during the leg extension component of courtship, resulting in an "abbreviated leg extension." The effect of both changes was to reduce the possibility of contacting the female during courtship. In this species, contact resulting from courtship is initiated by the female, never the male (Rovner 1968). It is of interest that, at a closer approach distance (2 MBL, 22 mm), blind courting males also switched to a tightened courtship posture and abbreviated leg extensions.

Stationary male detecting a non-approaching female.—If the female performed a turn or walked at a perpendicular or oblique angle to the motionless male's body axis (at a faster than cryptic speed), the male usually responded by a full turn to face directly toward her. This occurred in sighted males at up to at least about 5 MBL (61 mm), but in blind males at only up to about 2 MBL (22 mm). Blind males could respond at greater distances of up to about 4 MBL (46 mm), but only with partial turns, i.e., they were not yet facing the female at the completion of the turn. Thus, vision provided for a more accurate orientation response at a greater distance than did mechanoreception.

Moving male encountering a cryptically moving or motionless female.—When wandering, neither sighted males nor blind males could detect very slowly moving or motionless females. Males often approached such females to near or actual contact, even if the female adopted a vertical extend agonistic posture (Nossek & Rovner 1984) during the male's approach (Fig. 2). Such data suggested that moving males could not readily detect stationary females performing postural and/or appendage position changes and that they lacked form vision. Also, there apparently was no close-range, airborne pheromone produced by the female. On the other hand, if the wandering male *R. rabida* finally contacted the female, he began courtship display within 0.3 sec. (Since males did the same after contacting other males, as described below, it was not certain that courtship onset following hetero-

Figure 2.—The wandering, sighted male *Rabidosa rabida* (at right) continued to approach the female, even though she performed the behavior of adopting a "vertical extend" posture while both spiders were nearly face to face during his approach.

sexual contact was dependent on a sex pheromone.)

Sighted stationary female responding to a moving male.—Sighted females performed full turns of up to 155° in response to the stimulus of a male walking across their field of view at distances of up to at least about 4 FBL (68 mm). They also performed such turns in response to the first leg I extension movement shown by a male that had just begun courting at up to at least about 3 FBL (55 mm) distance.

However, sighted females sometimes showed no response to the approach of a wandering male at what seemed to be greater than cryptic speed coming from any of various directions. This resulted in the male almost contacting her nearest leg before she performed a flexion of that leg or some stronger response. In such cases, the female's response was triggered when the male's leg I swept past her leg at 2–3 mm distance between surfaces. (Trichobothria probably were the receptors that detected the stimulus.) Occasionally, actual contact between the male and female legs occurred before the female responded.

Such near or actual contact between the spiders was least likely to occur when a wandering male waving his legs I happened to approach directly toward the female's face. When a leg I-waving male made such an approach toward the female and was about 1–2 FBL (21–32 mm) away from her, the female typically drew back into a horizontal flex posture (Nossek & Rovner 1984). If the male got closer (i.e., less than 1 FBL away) without initiating courtship, the female usually ran rapidly forward in an apparent attempt to capture him.

Such high-speed approaches by the female elicited a rapid running away by the male. Advancing females usually did not respond by turning in the direction of the departing male, but instead remained oriented toward the male's original location, toward which she had been running. In other words, the female failed to perform re-orientation responses that would have tracked the escaping male's rapidly changing location as he dashed to a new site in the arena. It is probable that, because of the female's own movements, her visual system could not perceive the rapid re-location of the fleeing male. Nonetheless, a few of the sighted females were able to pursue an escaping male.

Blind stationary female responding to a moving male.—Blind motionless females could detect walking males at up to only about 2 FBL (33 mm) distance. They also were more likely than sighted females to be involved in near or actual contacts by such males, since these females often did not respond to an approaching male unless directly contacted or unless his waving leg I swept to within 2–3 mm of one of their legs. Consequently, blind females sometimes were unresponsive to extremely close approaches by slowly wandering males (Fig. 3). On the other hand, a courting male was detected by blind females at up to at least about 3 FBL (58 mm). The females' response to such vibratory input was usually a partial turn, but sometimes they performed a full turn of up to 140° that resulted in their directly facing the male. This ability to use mechanoreceptive information for accurate orientation toward a stimulus located at a distance comparable to that for visually based orientation is dependent on the nature of the source, a courting male, whose acoustic signal exceeds the vibration amplitudes generated by a walking male.

In this study, blind females solicited and accepted copulation more readily than did sighted females: 90% (18/20) of the blind females copulated; 60% (12/20) of the sighted females copulated. A *t*-test of the arcsine-transformed

Figure 3.—The blind female *Rabidosa rabida* (facing right) remained motionless in a rest posture as the slowly wandering sighted male approached so closely that his legs I and II overlapped (but did not contact) her left legs and body.

Figure 4.—Blind male *Rabidosa rabida* displaying courtship toward one another following a brief contact.

percentages was significant at $P < 0.05$ ($t = 2.30$). Also, three of the sighted females cannibalized the male rather than permit copulation, while none of the blind females preyed on the male. Does the availability of the visual channel in the female increase the likelihood that she will respond to a non-courting male by an act of attempted predation? Or perhaps is the female being more selective ("choosier") in response to some type of visual information than she would be if her response were based purely on vibratory information?

MALE–MALE INTERACTIONS

Inability to detect cryptically moving or motionless individuals.—As noted above for male–female interactions, contact typically resulted from the inability of either blind or sighted spiders when wandering to detect a motionless spider at any distance, even one that adopted a horizontal flex posture when it was approached closely. Furthermore, when motionless, most of the blind spiders (65%), and even some of the sighted ones (35%), did not respond to a wandering spider that approached very slowly. Thus, accidental encounters were frequent, as were cases in which both spiders ended up in resting positions with overlapping but non-contacting legs. The latter occurred more commonly in pairings in which both spiders were blind than in pairings of sighted spiders, although the amount of resultant leg overlap was no different (sighted: 7.4 ± 0.92 mm ($n = 12$); blind: 8.4 ± 0.89 mm ($n = 17$), Mann-Whitney $U = 86$, $P > 0.05$). Thus, if the conspecific was motionless or moving very slowly, the onset of courtship or agonistic display required contact or near contact, even for some sighted spiders.

Accuracy of orientation turns.—If a motionless spider detected a moving conspecific, blind males were less able than sighted males to accurately perform a full turn to face the stimulus. In other words, most of the blind males (70%) performed partial turns. The proportion of orientation turns that reached the target direction was 39% (31/79) in blind males but almost twice that (75% = 38/51) in sighted males (for arcsine-transformed percentages, $t = 4.10$; $P < 0.001$). These data suggested that detection of distant vibrations via the metatarsal lyriform organs did not yield as precise an orientation response in male *R. rabida* as did visual input.

Courtship display as an initial response.—In 70% of the pairings that involved a sighted male, courtship display followed the sighted male's orientation toward the other male. In 50% of the pairings involving blind males, courtship display was the initial response of a blind male to brief contact or near contact (i.e., 2–3 mm between leg surfaces). Mutual courtship display was sometimes the initial interaction when two blind males encountered each other (Fig. 4); however, this did not occur when sighted males were involved, i.e., a sighted male did not court in

Figure 5.—Male *Rabidosa rabida* engaged in grappling, which involves pushing one another while maintaining prolonged contact of their legs I. Although not visible in this video image, the defensive mechanism of leg spine erection occurs in both spiders throughout such contact.

response to a courting male. These data indicated that: (1) As was probably true of females, males lacked a visual recognition mechanism for determining the sex of a conspecific that had not yet begun courtship display. (2) Males lacked a chemical recognition mechanism that sufficed for determining the sex of another male on the basis of a brief contact. (3) Once courtship had begun, the visual system was more effective than the mechanoreceptive system for recognizing that a conspecific was a male, i.e., seeing the leg I extension component of courtship display probably was a more effective source of information than was detection of the concurrent palpal-generated vibrations.

Agonistic display.—When one male did recognize that a nearby conspecific was also a male, the first male initiated agonistic display (Rovner 1968). Such recognition of the sex of the other spider could come from detecting the visual or acoustic components of a courting male's display. However, recognition was especially likely to result from the prolonged period of contact that occurred during "grappling," which was ritualized fighting characterized by mutual pushing while holding each other's legs I (Fig. 5).

The palpal-generated sounds characterizing agonistic display were louder than those produced during courtship display. On the basis of these agonistic display sounds, blind males could detect other males at a distance of up to at least 4.5 MBL (56 mm). This indicated that when the sighted males had responded to another male's agonistic display, I could not know if the response had been elicited primarily on the basis of vision or mechanoreception.

Lack of importance of vision for dominance.—In the 10 trials involving a sighted male paired with a blind male, the blind male turned out to be dominant in seven of the nine trials in which dominance was clearly established. (In these seven trials, the blind male was the larger individual in two trials, equal in size in four trials, and smaller in one trial.) The onset and nature of grappling behavior was similar in sighted and in blind males, and thus probably was mediated entirely by mechanical information during contact.

DISCUSSION

By experimentally shutting off the visual channel of information gathering, I was able to examine the effectiveness of the mechanoreceptive and chemoreceptive channels for mediating interactions between individuals of *R. rabida*. At distances of up to four male body lengths (46 mm), a blind motionless male could detect the vibrations of and accurately orient toward a female that was walking at a greater than cryptic speed. The detection of the presence of another male, whose lighter mass generated lower amplitude vibrations than did a female, tended to yield less accurate orientation, with partial turns occurring rather than full turns. Nonetheless, the ability of blind males to detect conspecifics at a distance and to perform withdrawal responses when females approached indicates that, whenever anyone is studying the interactions of wandering spiders, the responses of sighted males to conspecifics cannot be assumed to be visual but instead may be based partly or entirely on substratum vibrations. Over many years of observing this species, I had assumed that the tightened courtship posture and abbreviated leg extension were visually based responses. (Of course, at the greater distances at which they were shown by sighted males, they probably are visually based responses.) The point is that no conclusion as to which sense mediates a response can be drawn by simple observation of wolf spiders. An experimental ap-

proach eliminating one or the other sense is required.

The behavior of blind motionless females also was revealing. The distance at which they could detect walking males was less than half the distance achieved by sighted females. However, blind females could detect a courting male at almost twice the distance they could detect a walking male. Assuming that vision is inadequate under dim light (but see below), the relatively high-amplitude, patterned vibrations generated by a courting male would enable him to be identified at night by a female at a greater distance than that at which she could detect a wandering male.

Blind motionless females sometimes did not detect males that approached slowly. However, actual contact usually was avoided, probably because the female's trichbothria were stimulated by the wandering male's leg I waving at a near-field distance of 2–3 mm. This probable role for the trichobothria might have gone unnoticed by investigators working with sighted females, since the female's reaction would have been assumed to be based on visual stimulation.

A lack of form vision in *R. rabida* was suggested by the behavior of motionless sighted males, which "ignored" very slowly moving females. (Of course, the female avoided detection by being both vibrocryptic and visually cryptic.) Also providing evidence for a lack of form vision was the fact that wandering, sighted males approached and contacted stationary females. Males even continued to approach females that adopted a vertical extend posture when the male came within close range. This lack of response to the female's action may be due to the probability that a moving *R. rabida* does not readily detect a moving stimulus, which also was suggested to be the reason for the absence of a mirror-image response in these spiders (Rovner 1989). Such data call into question the widespread assumption that the defensive postures seen in many spiders, such as *R. rabida*'s vertical extend, are displays, i.e., behaviors that evolved partly or wholly for communication. Instead, in some species they may still serve purely to prepare the spider to use its chelicerae and fangs.

An unexpected finding of this study was the ineffectiveness of chemoreception for providing information about the sex of a conspecific. Unlike the females of various salticid spiders (Crane 1949), female *R. rabida* apparently do not produce an olfactory signal that enables males to detect females at close range (Fig. 3). (Tietjen (1979) had experimentally demonstrated the absence of a long-range olfactory pheromone in this species.) Actual contact was needed for a wandering male to be stimulated to court by a motionless female. Since males also showed courtship after briefly contacting other males, it is possible that *R. rabida* has a species-specific rather than a sex-specific pheromone. Or perhaps if contact is too brief, the opportunity for uptake of a pheromone by chemoreceptors is inadequate to provide for recognition. Then again, it is also possible that mechanoreception by itself can cause courtship onset.

What may be concluded overall about *R. rabida* is that vision (primarily) and mechanoreception (secondarily) play important roles in mediating interactions under daylight conditions, while the chemical sense may not be involved unless there is prolonged contact with a pheromone-bearing surface. The behavioral evidence obtained in the present study supports Land's original (1981) view that lycosids lack form vision. However, Suwa (1984) hypothesized that females of the lycosid species *Pardosa laura* Karsch 1879 use form vision for species discrimination. Of particular significance are recent physiological studies by Land & Barth (1992) and Strausfeld et al. (1993) on the related ctenid spider *Cupiennius salei* (Keyserling 1877), which point to a role for form vision via the principal (antero-median) eyes. Consequently, the possible involvement of form vision in mediating interactions in *R. rabida* and other lycosids must be explored in future behavioral investigations.

Data in the present study indicate that *R. rabida*'s visual system provides for more accurate directional information-gathering at a greater distance than does mechanoreception. Furthermore, the occurrence of mutual courtship in blind males but not in sighted males suggests that vision provides a more effective recognition mechanism than does mechanoreception. Nonetheless, the data obtained in the blind male–sighted male pairings show that mechanoreception alone is sufficient for the establishment and maintenance of dominance in *R. rabida*. Also, one would assume

mechanoreception to be the primary basis for gathering information about conspecifics during interactions at night. However, behavioral research on *R. rabida* is needed to assess the effectiveness of vision during nocturnal encounters. One must consider the possibility that a dark-adapted visual system in such a lycosid spider could be sensitive enough under very dim light conditions to continue to have the dominant role in mediating interactions that it played under daylight conditions in the present study. It is worth noting that visual sensitivity sufficient for functioning under moonlight has been described for the largely nocturnal ctenid *C.salei* (Barth et al. 1993).

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AGE-RELATED CHANGES IN MOVEMENT PATTERNS IN THE FISHING SPIDER, *DOLOMEDES TRITON* (ARANEAE, PISAURIDAE)

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ABSTRACT. Based on the pattern of movement used during the search for prey, predators can generally be placed into one of two categories: active or passive searchers. This study documents an age-related switch in the movement pattern of the pisaurid spider *Dolomedes triton*. Individual spiders were marked and followed during two consecutive seasons on two ponds at the Patuxent Wildlife Research Center in Laurel, Maryland. Mean distances moved per day were compared between adult females and juveniles. During both years, and on both ponds, adult females traveled significantly greater distances per day than did juveniles (1.88 ± 0.33 m *vs.* 0.19 ± 0.02 m for adult females and juveniles, respectively; years and ponds pooled). This shift suggests an age-related difference in foraging strategy. Repeated observations on individual female spiders support the notion that juvenile *D. triton* switch to a more active search mode upon maturation. It is hypothesized that this change in movement represents a switch in foraging strategy in response to increased energy requirements during yolk production.

It is generally regarded that predators search for prey by using one of two basic modes. "Ambush" searchers (Greene 1983; Gerritsen & Strickler 1977), also known as "sit-and-wait predators" (Huey & Pianka 1981; Pianka 1966) or "passive searchers" (Eckhardt 1979), remain stationary for long periods of time, waiting for prey to enter their field of perception. They contrast with animals that move continuously through the environment; these are known as "cruise predators" (Greene 1983; Gerritson & Strickler 1977), "widely foraging predators" (Huey & Pianka 1981; Pianka 1966), or "active searchers" (Eckhardt 1979). Web-building spiders have been offered as the exemplary sit-and-wait predator (Riechert & Luczak 1982). However, spiders differ in their residence times at a web-site, both within and between species. Prey availability and hunger have been implicated in the selection of, and tenacity at, foraging sites for many spiders (e.g., Turnbull 1964; Riechert & Tracy 1975; Gillespie 1981; Janetos 1982a, 1982b; Morse & Fritz 1982; Olive 1982; see Wise 1993 for a review). Two models attempting to explain this relationship have been developed and applied to web-building spiders: 1) Janetos' (1982a) adaptation of a patch-selection model from optimal foraging theory and 2) Caraco and Gillespie's (1986; Gillespie & Caraco 1987) risk sensitivity model.

The general spider models of Janetos and Caraco & Gillespie may not apply to many cursorial spiders. While crab spiders which hunt from discrete inflorescences are particularly amenable to analysis with patch-selection models of optimal foraging theory (e.g., Morse 1986, 1988; Morse & Fritz 1982, 1987), it may be difficult to apply this approach to spiders that do not use a discrete, well-defined site. Definitions of "site" and measurement of "site quality" are difficult when the boundaries themselves are ambiguous. Risk-sensitive models of movement assume that in a given habitat, the two strategies of active and passive foraging yield the same expected total number of prey but differ in

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their variance. This may be the case for a web forager, which builds a web and then must wait for prey to enter. However, rapid movement by wandering spiders may result in increased encounters with prey, perhaps by leading to additional types of prey in the diet (Huey & Pianka 1981; DeVita et al. 1982). This may result in differences in the means as well as the variances of the prey expected under each of the two strategies.

The lack of appropriate models or formal analyses of the foraging behavior of spiders that do not capture prey with webs is likely related to the general lack of substantial data. Few studies have rigorously examined movement and foraging modes among the cursorial spiders. Riechert & Luczak (1982) argue that cursorial spiders primarily employ a sit-and-wait strategy in foraging for food because of the need to conserve energy. They hypothesize that natural selection has favored individuals which minimize energy expenditure. Thus, even salticids, which are generally considered to be very active foragers, spend much of their time stationary on a substrate and orient to prey only when it enters the visual field of perception (Givens 1978).

Comparing different age classes of the same species may be a fruitful approach to understanding the environmental correlates of different foraging behaviors in spiders, since much of the confounding variation present in interspecific comparisons is absent. Researchers have seldom made clear distinctions between the possibly different selective constraints on foraging for prey of juvenile and adult spiders (with the exception of males, which switch to foraging for females upon maturation). Such distinctions may be important. An extreme example is the pisaurid *Pisaura mirabilis* Clerck in which juveniles use a prey-catching web, but adults actively hunt (Lenler-Eriksen 1969). Similar behavior has been attributed to species of the tetragnathid *Pachynatha* Sundevall (Gertsch 1979).

In this paper we report the discovery of a marked age-related change in the movement pattern of an entirely cursorial species, the fishing spider *Dolomedes triton* Walckenaer. We document the switch of juvenile females to a more active mode that occurs upon reaching sexual maturity, and then introduce the hypothesis that this ontogenetic change in behavior represents a switch in foraging strategy in response to increased energy requirements during yolk production.

METHODS

Biology of *D. triton*.—*D. triton* is a very large (body length: 0.9–2.5 cm) member of the family Pisauridae that occupies the shorelines of ponds and lakes throughout North America. Spiders of the genus *Dolomedes* Latreille, the most aquatic of the pisaurids, are able to run on and dive under the water surface in order to catch prey and escape predation. *D. triton* is a generalist predator, utilizing a wide prey spectrum. Rather than using webs, displacement of the water surface is used to detect and locate prey (Bleckmann & Barth 1984). Foraging is closely associated with vegetation. These spiders are typically observed resting on emergent vegetation with at least one leg contacting the water surface (Carico 1973; Bleckmann & Rovner 1984; pers. obs.). Vegetative sites provide not only a resting site during foraging, but also the support necessary for breaking surface tension during dives for predator avoidance (McAlister 1960).

Invertebrates active near or on the surface of the water are most likely to be taken as prey by *D. triton* (Zimmerman & Spence 1989). Prey items commonly are other pond predators, such as gerrids, notonectids, and odonates. Vertebrates such as tadpoles and small fish are sometimes eaten as well (Bleckmann & Lotz 1987). Additionally, Zimmerman & Spence (1989) report that all instars except the smallest juveniles and adult males are cannibalistic, feeding on conspecifics of smaller or similar size.

D. triton takes two years to reach sexual maturity (Carico 1973). Adults can be found between May and September in central Alberta, Canada (Zimmerman & Spence 1989, 1992) and between April and November in Maryland, USA (pers. obs.). Juvenile *D. triton* overwinter among debris and vegetation close to the margins of ponds and lakes (Bishop 1924; Kaston 1948). Zimmerman & Spence (1989, 1992) report that overwintering juveniles reinvade the water surface as soon as the ice melts, when they commence feeding and reach the adult stage after an additional 2–3 molts.

Study area.—The spiders were observed on two artificial freshwater ponds located in

the Patuxent Wildlife Research Center in Laurel, Maryland. Bluegill Pond is approximately 150 m × 45 m with an average depth of about 1.1 m. Marginal vegetation primarily consists of *Sparganium americanum* (burreed), *Eleocharis quadrangulata* (square-stem spikerush), *Scirpus cyperinus* (woolgrass), *Juncus effusus* (softrush), *Nuphar luteum* (spatterdock), *Nymphaea odorata* (white waterlily), *Polygonum hydropiperoides* (swamp smartweed), and two large stands of *Saururus cernuus* (lizardtail). Farm Pond is approximately 60 m × 60 m, with an average depth of 2 m. Principal marginal vegetation consists of *Eleocharis quadrangulata, Potamogeton diversifolius* (pondweed), *Liquidamber styraciflua* (sweetgum), *Polygonum hydropiperoides* and *Juncus effusus.*

In 1991, 35 m of the north margin of Bluegill Pond were partitioned into 1 m^2 quadrats by staking with bamboo poles. In June 1992, the south and east margins of Farm Pond were similarly demarcated. Maps displaying the features of the ponds' perimeters, including vegetation, were created and used to identify and record locations of *D. triton.*

Data collection and analysis.—The partitioned area of Bluegill Pond was searched for spiders at least three times per week from 11 July–15 October 1991 and from 23 April–29 June 1992. In July 1992 the dam on this pond broke and the pond was almost completely drained. Consequently, the study was moved to Farm Pond and continued from 12 July–3 November 1992.

Searching involved slowly wading around the perimeter of the ponds or paddling in a rubber boat. The location of each spider sighted was recorded on a map. Other information, such as the activity of the spider, the vegetation it was touching, and its posture in relation to that vegetation, was also recorded. Some spiders were captured, measured, and their carapace marked with Liquitex® acrylic paint for identification. Marks were applied with a thin paintbrush using the 1–2–4 marking code described by Zimmerman & Spence (1982). Marked spiders were returned to the same site from which they were taken. This approach provided both a cross-sectional sample of habitat use by the population and longitudinal mark-recapture data on a portion of the population. Spiders were remarked with the same identifying number following a molt only if the spider was found in close proximity to the exoskeleton and displayed the characteristic greenish cast of a newly molted individual (Zimmerman & Spence 1982; pers. obs.). Additionally, missing and regrown appendages were used to assist identification.

When marked spiders were resighted, the mean distance moved per day was conservatively calculated by assuming that spiders moved in a straight line from the previously sampled point, and then dividing by the number of days since the last sighting. Additionally, the distances of each resighting from the point of the initial sighting were calculated as an estimate of the range of movement. These methods of measurement only indirectly reflect activity levels, but in the absence of continuous monitoring, provide an approximation of movement. Although all age and sex classes were marked, adult males were excluded from the analyses. Adult male *D. triton* are rarely found feeding (Zimmerman & Spence 1989) and their movements probably reflect mating rather than feeding activities.

RESULTS

During both years, and on both ponds, adult females traveled *ca.* 10 times farther per day than did juveniles (Table 1). Juveniles and adult females also differed markedly in their total range of movement, estimated for resighted spiders as the distance from the first sighting (Fig. 1). Early in the season, only juveniles were present on the pond, and very little movement was evident. During the midseason, when juveniles and adults coexist, the contrast between the two age classes was dramatic. Juveniles continued to move very little while females were considerably more active. In late fall, after the adults had died, increased movement by juveniles was observed. This is likely to be due to overwintering activity, rather than foraging, since these spiders were often found on the shore itself under dried vegetation. Farm Pond was also equipped with an overflow drain, which created a directional flow of water during wet periods. This flow may have affected juvenile movement as well. The fall movement was not observed the previous year on Bluegill Pond.

Although adult females are generally larger than juveniles, the increased movement is not strictly associated with the adults' larger size (Fig. 2). The largest juveniles do not move

Table 1.—Mean meters moved per day by juvenile and adult female *Dolomedes triton* without egg-sacs. In order to make the analyses from the two ponds comparable, only the data collected between 1 July and 31 October were analyzed. *T*-tests adjusted for unequal variances were used to compare the mean distances for juvenile and adult females.

		n	Mean distance (m)	SE	*P*
1991 Bluegill pond	Juveniles	7	0.10	0.02	
	Adult females	24	1.83	0.52	0.003
1992 Farm pond	Juveniles	59	0.20	0.02	
	Adult females	16	1.94	0.28	0.0001

significantly more than small juveniles, despite a carapace width that is indistinguishable from adult females. Likewise, adult females with small carapace widths do not move less than those with large carapaces. Maturity, rather than carapace width, predicts the mean distance moved (MANOVA, $P < 0.05$).

The behavioral change in movement pattern is correlated with the occurrence of the last molt (Figs. 3–6). Before molting, penultimate females exhibited the typical juvenile pattern of movement. Following molting, a sharp increase in movement occurred. The increase in activity did not simply take place within a home range, as indicated by the distance moved from first sighting. The spiders moved considerably until the egg sac was constructed. Once the egg sac was formed, females moved much less and resumed a pattern characteristic of juveniles. The mean distance moved per day by females with egg sacs was 0.19 ± 0.03 m ($n = 18$; 1991 observations in Bluegill Pond). In contrast with juveniles, females with egg sacs were never observed feeding. Egg sacs were continuously held in the chelicerae until hatching.

Thirty-two nursery webs were examined at Bluegill Pond in 1991. Forty-seven percent of

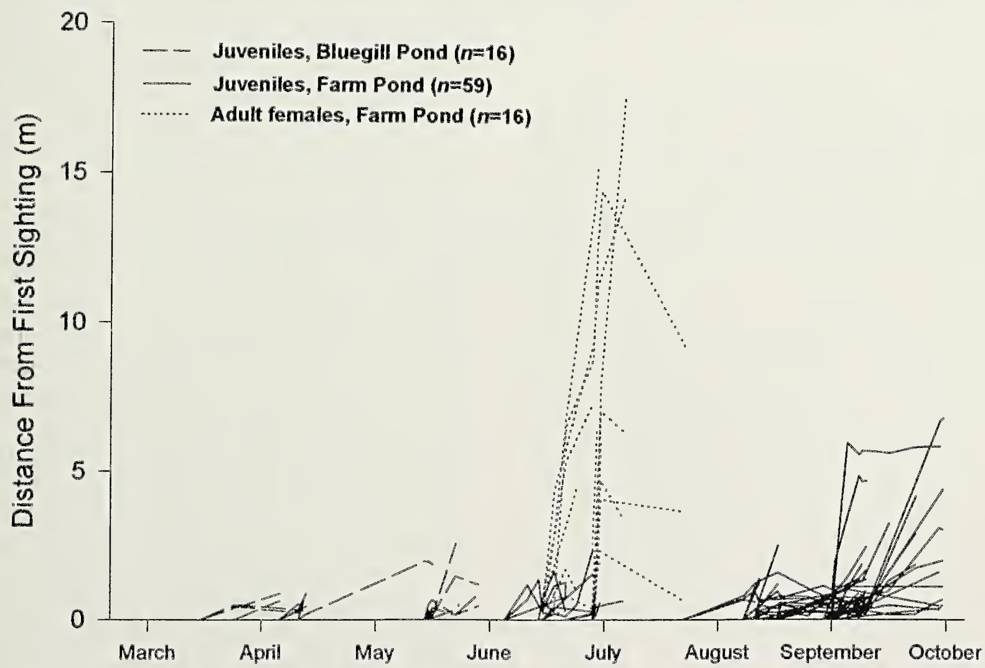


Figure 1.—Distances moved from the first sighting of juvenile and adult female *Dolomedes triton* in 1992 during the early season on Bluegill Pond and mid-late season on Farm Pond.

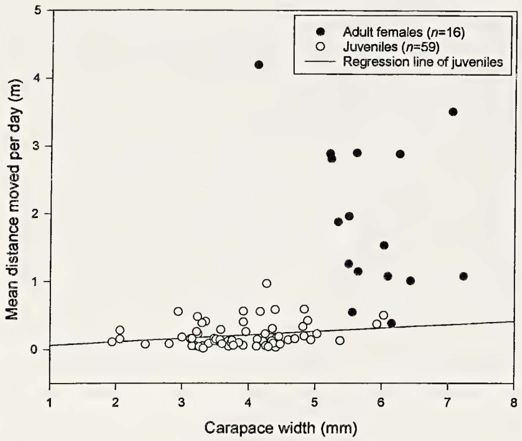


Figure 2.—Mean distances moved per day in meters as a function of carapace width for both juvenile and adult female *Dolomedes triton* without egg sacs. The regression line of the juveniles is shown.

the webs were built exclusively in soft rushes (*J. effusus*), and another 19% were built in rushes together with another species of plant. Most other plant species (e.g., burreeds, woolgrass, grasses) that were used by females for nursery webs were similar to *Juncus,* with linear, grasslike leaves. While shrubs and herbs such as lizardtail (*S. cernuus*) and smartweed (*P. hydropiperoides*) are plentiful at the pond's perimeter, they were rarely used for nursery webs.

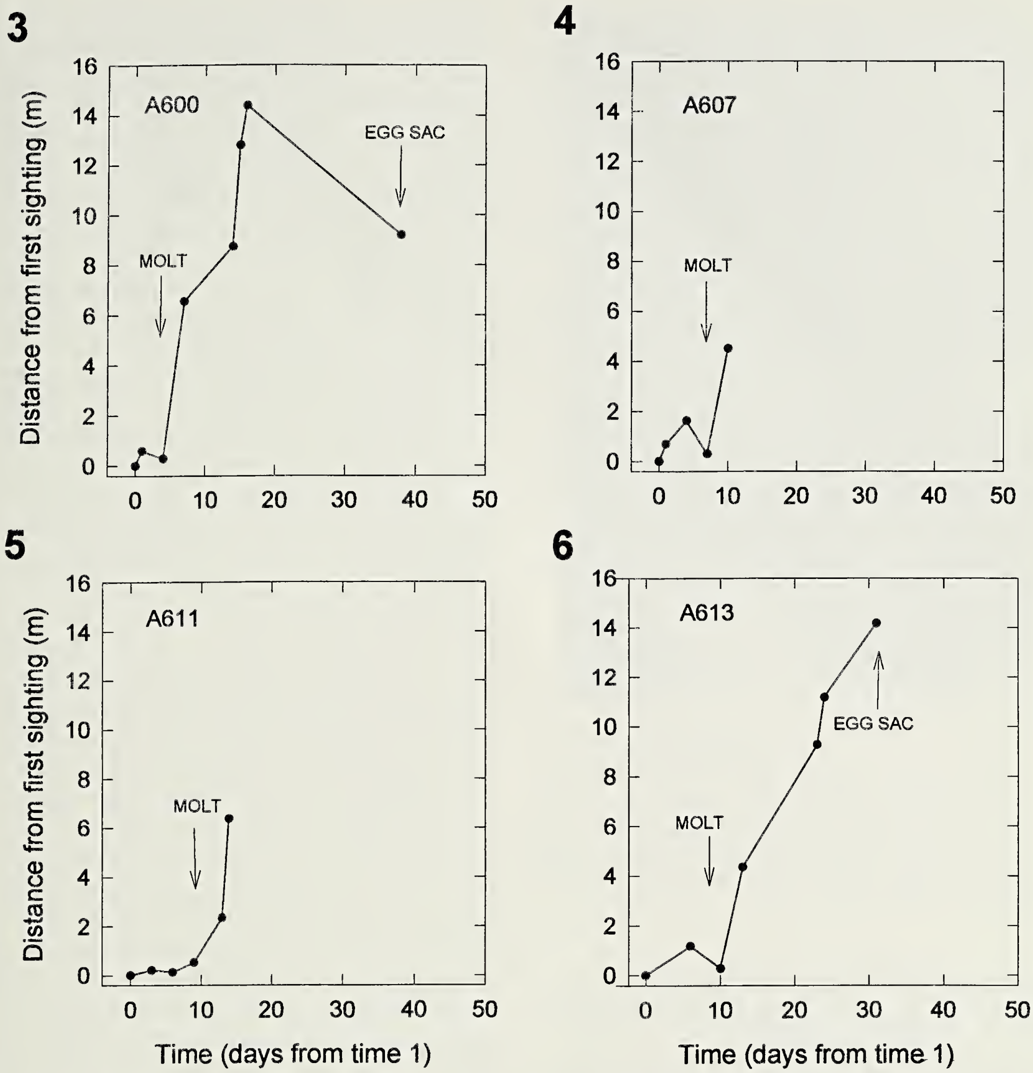
DISCUSSION

We have found evidence in the fishing spider for an age-related switch in movement pattern. Juveniles clearly employ a sedentary strategy throughout much of the year. Following their last molt, newly-adult females switch to an active period characterized by frequent movement. Presumably, increased movement by spiders also increases their exposure to predators (e.g., Vollrath 1985). Increased movement also incurs a greater metabolic cost. Studies with wolf spiders show that active metabolic rates are *ca.* 3–4.5× resting rates (Miyashita 1969; Ford 1977; McQueen 1980). Thus, metabolic costs may play a significant role in foraging decisions by cursorial spiders, especially when coupled with the likely increase in predation risk. These costs must be offset by benefits in order for increased movement to be an adaptive behavioral option.

Norberg (1977) was among the first to apply optimal foraging theory to the selection of foraging modes. He contrasts a foraging mode with a high feeding efficiency but high energetic costs (mobile strategy) to one in which both feeding efficiency and costs are low (sit-and-wait strategy). Norberg's model minimizes daily foraging time, and predicts that predators should switch from high-efficiency, high-cost modes to low-efficiency, low-cost modes as prey densities, and thus energy resources, decline. While one of the most frequently observed shifts in foraging mode is indeed prey-density dependent, it is often in the opposite direction from Norberg's predictions. Many species switch from ambushing at high prey densities to active searching at low prey densities (e.g., diving beetle, Formanowicz 1982; water scavenger beetle larvae, Formanowicz et al. 1982; centipedes, Formanowicz & Bradley 1987; odonate larvae, Johnson & Crowley 1980; salamander, Jaeger & Barnard 1981). Helfman (1990) notes that each of these apparent contradictions to Norberg's predictions are ectothermic animals. He proposes that ectotherms, with relatively low metabolic needs and costs of activity, may behave to maintain a minimum encounter rate with prey. Endotherms, with higher metabolic energy requirements, may behave to maximize the ratio of energetic return to expense as Norberg's model predicts.

Formanowicz & Bradley (1987) argue that a more active strategy is utilized to increase the probability of finding prey when a predator has the greatest need to acquire energy, irrespective of cost. Support for this comes from studies which have shown hunger to be important in the foraging movements of a mantid (Inoue & Matsura 1983) and ant-lion larvae (Griffiths 1980). Both of these invertebrate predators employ an ambush strategy for prey capture, making frequent site changes as hunger increases. As Helfman (1990) points out, this situation is analogous to traditional optimal diet-selection models (e.g., Krebs & McCleery 1984), which predict a decline in prey selectivity as prey densities decrease. In both cases, predators are willing to expend more energy for an increased probability of successful intake of energy, while avoiding cheaper alternatives that entail a greater probability of failure.

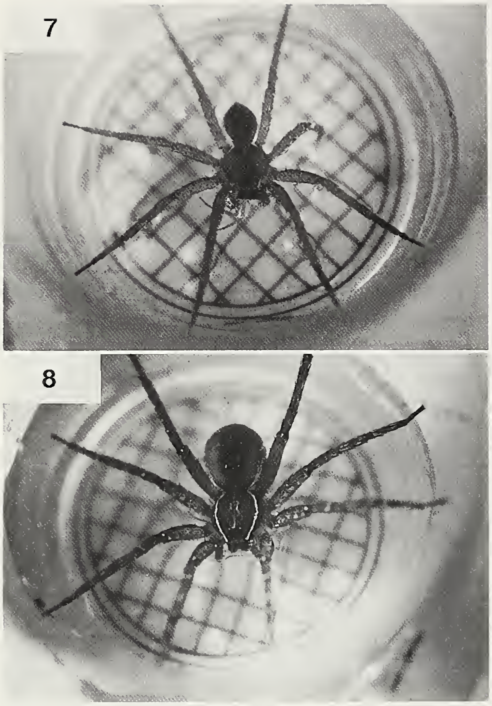
It is likely that during the period between the last molt and egg sac formation, the en-



Figures 3–6.—The distance (in meters) from the first sighting for the four adult females for which data is available at least five days prior to the molt to adulthood.

ergy demands in adult female *D. triton* greatly increase, due largely to the accumulation of yolk in the eggs. Generally, yolk accumulation in spiders occurs in two steps (Seitz 1971, as cited in Foelix 1982). At first, fine-grained yolk particles aggregate in the young egg cell. After copulation, a second accumulation of yolk begins, this time in the form of much larger granules. In the cursorial spider *Cupiennius salei* Keys, egg cells increase ten- to twelve-fold in size during yolk accumulation, and the female's abdomen visibly swells. This second phase can take place only if enough food is available (Foelix 1982). Zimmerman & Spence (1989, 1992) note that female *D. triton* feed intensively and are extremely cannibalistic following mating. Pronounced abdominal swelling during this period is evident in *D. triton* as well (see Figs. 7, 8).

The period of yolk accumulation is a time when foraging returns are extremely important. Field experiments supplementing the food of other species of female spiders have demonstrated that additional food results in increased fecundity (e.g., Wise 1975, 1979; Spiller 1984; see Wise 1993 for a review). Little information is available on the degree of food limitation in *D. triton*, but it seems likely



Figures 7–8.—Two adult female *Dolomedes triton* with similar carapace widths. The difference in abdominal size is notable. The female in the top photograph recently shed and has just begun yolk accumulation in the eggs, while the female in the bottom photograph is near the time of egg-sac construction.

that increased energy demands play an important role in its foraging strategy during the period of yolk production.

Why don't juveniles adopt a more active strategy for foraging? Food limitation of juveniles may have delayed effects upon fecundity, possibly due to a decreased capacity to carry eggs. For example, Schoener (1971) argues that increased food intake can affect reproductive output not only directly through size or number of eggs, but also by increasing the size of the parent, particularly when egg number is directly proportional to body size. Supplementing prey of juvenile spiders in natural populations has been demonstrated to result in increased growth (Wise 1975, 1983), and a strong correlation has also been found between size at maturity and egg production in spiders (e.g., Petersen 1950; Wise 1976; Wise & Wagner 1992). Thus, securing additional food during the juvenile stages should increase potential fecundity. Nevertheless, the sit-and-wait foraging style of juvenile *D. triton* is closer to what Riechert & Luczak (1982) predict for spiders minimizing energy expenditure. One possible explanation for this comes from simple prey-encounter models (DeVita et al. 1982) which predict limited benefit from an active foraging strategy if the prey are small and fast species. It is not known, though, whether the strategy of the juveniles is due to the type of prey sought, or whether the prey type captured are a result of a sedentary foraging strategy.

Increased food acquisition is not the exclusive tenable hypothesis for the observed age-related difference in movement. Two alternative hypotheses are (1) evaluation of sites for egg-sac construction and nursery-web placement, and (2) differential predation pressures. The preference we found for placing the nursery web in *J. effusus* suggests that the site of egg construction is not random. As noted above, female *D. triton* carrying egg sacs move very little, spending approximately 3–4 weeks without food as they tend their egg sac. Once the egg sac begins to hatch, the nursery web is placed in the vegetation in the immediate vicinity. Selection of a site for the nursery web must therefore take place prior to sac construction. Aside from the structural properties of the vegetation, other features which may be important include predatory risks, density of conspecifics, and abiotic factors (e.g., temperature, humidity, the presence of wind-generated waves). Although these features may play a role in the final selection of a site, they are unlikely to be determining factors in the observed increase in activity of adult females. If the movement is driven by a search for an appropriate site, females would be expected to encounter appropriate sites at random periods of time following mating. Thus, some females should locate superior sites the day after their last molt, after which they should stop moving and thereby conserve energy, particularly if superior sites are limited. This pattern was not observed in the field during 1991 and 1992. Rather, females continued to move until egg-sac construction.

Differential predation pressures on adults and juveniles could play a role in causing the different movement patterns of the two ages, although rates of mortality from predation are not known for *D. triton*. Predation by fish during 1991 and 1992 was documented several

times as individuals moved across open water. An instance was reported by Carico (1973) in which a number of *D. triton* were found in the gut of an immature little blue heron (*Florida caerulea*), a species known to use a visual hunting style. Roble (1985) reports predation on *D. triton* by pompilid wasps, which also hunt visually. Great blue herons (*Ardea herodias*) were commonly seen hunting along the shores in the ponds at our study sites, but pompilid wasps have not been observed. Juvenile and adult female spiders are probably equally subject to predation by vertebrate predators such as wading birds, fish and frogs. However, the increased size of the adult females might make them less likely to be prey of other invertebrate predators of the pond. The risk of cannibalism is also probably higher for the juvenile age class. The switch to increased movement is not gradual, though, as might be expected if release from predation pressures due to size were solely responsible. Instead, the change from sedentary to active foraging takes place only after the final molt. Furthermore, the fact that juveniles remain stationary through August, September, and at least part of October, when few adult females remain on the pond, suggests that juveniles are averse to movement even in the absence of a potential major predator.

In summary, an age-related switch in movement patterns was observed in *D. triton*. It is argued that this switch represents a change in the foraging mode of adult females from sit-and-wait to active forager. It is hypothesized that this change occurs because the active mode provides a higher rate of energy gain, which is needed to meet the increased energy requirements of yolk production. Although an active strategy is metabolically more costly and results in increased exposure to predators, it may be necessary to ensure enough energy for egg production.

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THE RELATIVE ABUNDANCE OF *BROTHEAS AMAZONICUS* (CHACTIDAE, SCORPIONES) IN DIFFERENT HABITAT TYPES OF A CENTRAL AMAZON RAINFOREST

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ABSTRACT. During a nine week period, we studied the surface abundance of the scorpion *Brotheas amazonicus*, using 1200 pitfall traps arranged along eight line transects within each of three habitat types in a neotropical rainforest. We collected 193 scorpions of this species. Capture rates in the primary plateau forest and in the primary forest on white sand soil were higher than in disturbed areas. Structural habitat parameters in the vicinity of the trap lines (such as quantity of soil surface litter, number of stemless palms, dead wood and termite mounds on the ground) significantly differed among habitats. Disturbed areas showed lower structural diversity. In a regression analysis the measured habitat parameters proved to affect the abundance of *B. amazonicus*. We conclude that high structural diversity, ultimately reflecting the availability of hiding places, is important for this scorpion species. This is probably influenced by the predation pressure exerted by the highly diverse predator community in central Amazon terra firme forests.

In 1993 we spent three months in the Amazon studying spider ecology in a rainforest reserve near Manaus. We planned to do a study of the abundance of rainforest scorpions because these are frequently observed in all strata and microhabitats where spiders are studied and potentially interfere with spiders by competition and/or intraguild predation (Polis 1990). By preliminary sampling with pitfall traps and ground-photoeclectors, eight species of scorpions were collected in the study area. *Tityus metuendus* Pocock, *T. raquelae* Lourenço and *T. silvestris* Pocock are considered to live in the lower vegetation and trunk region, and *Ananteris dekeyseri* Lourenço, *A. pydanieli* Lourenço and *Chactopsis amazonicus* Lourenço & Francke apparently inhabit the litter (Lourenço 1988). An undescribed species of *Brotheas* cannot yet be classified ecologically because of its scarcity. The largest species, *Brotheas amazonicus* Lourenço, was commonly found under dead wood on the ground, in burrows on the ground, in termite mounds and embankments, and in litter accumulations in the base of stemless palms. *Brotheas amazonicus* was the only species collected in sufficient numbers by pitfall traps to allow correlations with habitat characteristics.

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METHODS

Site description.—The study was carried out from August to October 1993 in the "Reserva Florestal Adolfo Ducke" (RD), a reserve of the "Instituto Nacional de Pesquisas da Amazônia" (INPA), 26 km northeast of Manaus (03°08′S 60°02′W). The reserve is 10 km² and is covered by non-inundated terra firme rainforest. In the Reserva Ducke, two main forest habitat types occur (Guillaumet 1987). The main habitat, herein called plateau forest, is a primary rainforest with trees to 45 m in height on a typical terra firme clayey latosol. These forests are relatively poor in epiphytes, and lower vegetation is dominated by stemless palms of the genera *Astrocaryum* and *Attalea* (Prance 1990). A dense but lower "campinarana" forest occurs on white sand soils (tropical podsol), characterized by the trees *Rhabdodendron macrophyllum* (Rhabdodendraceae), *Pagamea macrophylla* (Rubiaceae) and *Humiria balsamifera* (Humiriaceae). Epiphytes (Bromeliaceae) are more abundant. For comparison, we choose several disturbed sites near the station buildings at the border of the

Table 1.—Capture rates of *Brotheas amazonicus* and measured habitat parameters per transect line in three different habitat types (if not otherwise stated numbers are individual counts).

Transect lines	1	2	3	4	5	6	7	8	Total	Mean	s
Plateau											
Specimens	7	8	7	9	12	16	22	17	98	12.25	5.55
Litter [cm]	14.8	8.3	10.0	14.3	12.7	15.0	18.5	19.8	113.4	14.18	3.88
Termitarias	2	3	4	1	4	4	5	2	25	3.1	1.36
Trunks	15	12	20	14	16	16	23	13	129	16.1	3.68
Palms	6	3	1	16	0	30	32	37	125	15.6	15.31
Campinarana											
Specimens	12	8	5	13	15	6	3	9	71	8.9	4.19
Litter [cm]	21.2	22.3	22.3	21.2	27.3	16.5	17.7	18.5	167.0	20.9	3.40
Termitarias	0	0	1	1	0	0	2	2	6	0.75	0.89
Trunks	19	14	17	13	13	11	7	7	101	12.6	4.27
Palms	4	0	3	20	1	0	1	0	29	3.6	6.78
Disturbed areas											
Specimens	2	2	1	4	7	5	1	2	24	3.0	2.14
Litter [cm]	0	7.7	0	11.5	12.2	6.7	0	15.5	53.6	6.7	6.17
Termitarias	0	0	0	0	1	0	0	2	3	0.4	0.74
Trunks	10	1	4	12	34	1	0	0	62	7.8	11.58
Palms	0	0	1	6	3	2	1	13	26	3.3	4.40

reserve. These do not represent a distinct habitat, but can be characterized by secondary vegetation, more exposed soil surfaces and more sandy soils.

Mean annual rainfall in the Manaus region is 2542 mm, and July–September are the driest months with generally less than 100 mm per month (Ribeiro & Adis 1984).

Sampling procedures.—Collections were made by pitfall traps, consisting of commercially available plastic cups (11.6 cm deep, opening diameter 10 cm), buried flush with the soil surface. Between 4–25 August traps were filled with picric acid. Later (until 2 October) traps were left without preservatives tc avoid killing non-target animals. Small holes were made in the bottom of the cups to prevent them from being filled with rainwater. Traps were then inspected daily, and scorpions were collected alive but later transferred to 70% ethanol. Previous observations indicated that scorpions were unable to escape from the cups, except when branches or leaves had filled them.

Capture rates of pitfall traps are clearly activity-based and therefore do not represent pure density data. However, in this study where capture rates for only one species from nearby sites over a short period are compared, we do not expect major variations or changes in activity and therefore consider the capture rates to be good indicators of relative scorpion abundance.

Pitfall traps were deployed in straight lines of 50 m, each line containing 50 cups at intervals of 1 m. Eight line transects were distributed in each of the two habitat types described above and in disturbed areas (total of 24 transects), thus every habitat type was supplied with 400 traps. Line transects were usually separated by more than 100 m, but some of them were less than 50 m apart.

During the study scorpions were regularly observed in the field, collected alive, and held in captivity to observe behavior.

Habitat parameters.—Within an area 10 m × 50 m along each of the transect lines, structural habitat characteristics were recorded. These included the number of termite mounds of *Cornitermes* sp.(> 10 × 10 cm = termitarias), the number of dead wood fragments on the ground (diameter > 10 cm and length > 50 cm = trunks) and the number of stemless palms (higher than 1 m). To measure litter quantitatively, six samples of 1 m² were collected in each of the 24 transect areas and the volume estimated by pressing the litter samples in a bucket of known size and measuring the height of the column.

Statistical tests were made using the program STUDENT SYSTAT (Berk 1994).

Table 2.—Comparison of habitat types by measured habitat characteristics (Kruskal-Wallis test statistic = H; *df* = degrees of freedom; + = significant at 5%, ++ = significant at 1%, +++ = significant at 0.1%; reject/accept = reject or accept the hypothesis of equal population means).

Comparison of habitat types by	H	*df*	Probability *P*	Significance	Conclusion
Litter	15.9	2	0.000	+++	Reject
Palms	4.27	2	0.118	–	Accept
Termitarias	13.6	2	0.001	++	Reject
Trunks	8.2	2	0.016	+	Reject

RESULTS

Capture rates.—From the 1200 pitfall traps 211 scorpions were collected. *Brotheas amazonicus* was by far the most abundant species with 193 specimens collected. There were 98 specimens collected in the plateau area, 71 in the campinarana and 24 in disturbed areas (Table 1). The sex ratio (males : females) in traps was 2.9 : 1. Other species collected were *Chactopsis amazonicus* (8 specimens), *Tityus metuendus* (7), *T. silvestris* (2) and *Ananteris sp.* (1). During the first three weeks, 78 specimens of *B. amazonicus* were sampled in pitfall traps with picric acid; during the following 5.5 weeks, 115 scorpions were sampled in traps without preservative liquid.

Differences in number of *Brotheas* scorpions between habitats were significant (Kruskall Wallis test statistic = 13.3 > chi-square 0.5, *df* 2, *P* = 0.001). The nonparametric multiple comparison (Tukey-type, see Zar 1984) ranked the number of scorpions per habitat as follows: disturbed area < campinarana = plateau.

Habitat characteristics.—All habitat characteristics, (i. e., the number of palm bases, dead trunks, termitarias and litter quantity) varied considerably within the habitats (Table 1) but are also significantly different among habitats (except palms; Table 2). From differences in rank sums of the nonparametric Kruskal-Wallis test, we see that the plateau differs from the other two habitats in all measured characteristics. The transects in disturbed areas showed higher variabilities in nearly all measured parameters and differed significantly only in litter quantity and number of dead trunks from the campinarana. In regression analyses all measured habitat characteristics (variables) proved to affect the abundance of *B. amazonicus* (Table 3). However, some of these variables were highly influenced by the habitat (e. g., termitarias and trunks). When habitat was included in the model for each factor, the proportion of variance explained by each factor was lower in the case of litter and palms, but higher in the case of termitarias and trunks. Thus including litter and palms as covariates improved the analysis of variance (Table 3).

Natural history of *Brotheas amazonicus*.—The scorpion species appears strictly nocturnal. Only one specimen was observed during the day – on a wall of the station only a few centimeters from his burrow. Many scorpions were observed, often close to burrows of theraphosid spiders (*Ephebopus uatuman*), in burrows on the embankment of an unpaved road entering the reserve. Burrows typically have oval, nearly elliptical openings and reach 20 cm depth. At night (observed from 2000–0200 h) the scorpions sit in wait for prey directly in the burrow openings, with only the pedipalps reaching forward most of the time. One specimen was observed taking possession of the burrow of a *Tityus metuendus*. Overall 33% of all captured females were gravid (embryos visible): 6 of 20

Table 3.—Regression analysis of number of scorpions (*Brotheas amazonicus*) by habitat characteristics with and without habitat included (+ = significant at 5%, ++ = significant at 1%, +++ = significant at 0.1%).

Variable	*P*	Significant	Variable + covariate	*P*	Significant
Litter	0.002	++	Habitat + litter	0.006	++
Palms	0.000	+++	Habitat + palms	0.001	++
Termitarias	0.006	++	Habitat + termitarias	0.447	–
Trunks	0.007	++	Habitat + trunks	0.101	–
Habitat	0.032	+			

females in the campinarana, 7 of 22 in the plateau forest and 3 of 7 in the disturbed areas. One gravid female was observed waiting for prey during three consecutive nights, then disappeared for three nights and reappeared carrying newborn scorpions. In the following 14 days this female appeared on an average of every second night at the entrance of the burrow, resting in a position where the pedipalps nearly closed the opening and responding to the slightest disturbance by retreating. In contrast to *Tityus* scorpions, *B. amazonicus* was never observed above the forest ground and appeared in arboreal funnel traps (3 m high on trunks) only when army ants (*Eciton burchelli*) had hunted on the ground below the trunks.

DISCUSSION

With eight scorpion species living sympatrically in the study area, Reserva Ducke is among the sites with the most diverse scorpion communities and the site of the greatest diversity outside of desert areas (Polis 1990). The apparent dominance of one species, *Brotheas amazonicus*, is probably biased by the capture method because we know that at least some of the other species live in higher strata. Between 7–22 *B. amazonicus* scorpions were sampled per line transect in the plateau forest (Table 1). The sex ratio in the traps, compared with actual sex ratios in Polis (1990) is certainly reflecting the fact that males are more vagrant (probably looking for females; see Polis 1990 and Polis & Sissom 1990). We considered the low level of surface activity of most scorpions (Polis 1990), our own observations for this species, and the greater activity ranges for males (3 m from burrow, 1 m for females) during the reproduction period to calculate very rough abundances of *B. amazonicus* in the plateau forest: 9.5/300 m^2 (males) and 2.75/100 m^2 (females), leading to an overall density estimate of 0.06/m^2. During our spider study we used five ground-photeclectors, each covering one m^2 of plant-free, litter-covered soil surface, and moved them every four weeks during the 12 months to another place within an area of approximately 10 ha. Thus from 60 m^2 covered by these traps, nine *B. amazonicus* were collected. The resulting density estimate of 0.15/m^2 is certainly still an underestimate because the scorpions apparently prefer to hide in habitat structures, which were not covered by traps. The only abundance value for a neotropical forest scorpion species available for comparison is 0.40/m^2 for *Centruroides margaritatus* (Gervais) in Costa Rica (unpubl. data in Polis 1990).

Despite significant differences in habitat characteristics between campinarana and plateau forest, differences in capture rates of the scorpion species were not significant. Sampling actual abundance might show differences better than activity-based pitfall trapping. Capture rates at the disturbed sites were significantly lower than in forest sites. Although some habitat characteristics of these sites were different from the forest sites, they do not represent a distinct habitat type, which explains the high variability of the measured parameters.

All studied habitat characteristics showed significant correlations with the abundance of the scorpion species under study. Hiding places such as soil surface litter, litter accumulations in palm bases, dead trunks and termitarias seem very important resources for scorpions. We presume predation to be mainly responsible for this. Juveniles of *B. amazonicus* (and of other scorpion species) were several times observed as prey of the army ant *Eciton burchelli*. Adults were found in arboreal funnel traps apparently driven away from the ground by hunting swarms of army ants. In a study of the prey spectrum of two swarm raiding army ant species (*E. burchelli* and *Labidus praedator*) in the Manaus region, scorpions made up about 3% of all prey fragments (Vieira & Höfer 1994). Fragments of scorpions were found in stomach contents of several frogs and lizards (*Leptodactylus pentadactylus* - Galatti 1992; *Uranoscodon superciliosa* - Gasnier et al. 1994) living in our study area. The predator community of Reserva Ducke is highly diverse: three species of arthropod hunting army ants (Vieira & Höfer 1994), 14 species of large cursorial spiders (Höfer et al. 1994), more than 40 species of frogs (Zimmermann & Rodrigues 1990), about 20 species of lizards (Zimmermann & Rodrigues 1990), more than 80 understory insectivorous bird species (Bierregard 1990) and more than 60 non-flying mammals (Malcolm 1990) live in central Amazonian terra firme forests. Most of these predators are generalized insectivores and are potential predators of scorpions.

In general view of the measured habitat parameters, the plateau forest seems to contain more structural diversity than the campinarana sites and certainly more than the disturbed sites. Other habitat characteristics (e. g., climatic factors,

soil humidity, soil hardness, and sandy condition of the soils) might also be important, but their importance remained undetected under "habitat" in the regression analyses.

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USE OF COLEOPTERAN PREY BY *PHIDIPPUS AUDAX* (ARANEAE, SALTICIDAE) IN TALLGRASS PRAIRIE WETLANDS

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ABSTRACT. *Phidippus audax* (Hentz 1845) was observed in the field and tested in a laboratory in order to estimate its use of two locally abundant, soft-bodied coleopteran species, *Diabrotica undecimpunctata* (Chrysomelidae, Galerucinae) and *Chauliognathus pennsylvanicus* (Cantharidae). In the field, *Phidippus audax* was most commonly observed hunting on leaves or stems of the common milkweed and feeding upon species of Diptera or *Diabrotica undecimpunctata.* Despite high densities of *Chauliognathus pennsylvanicus, P. audax* was never observed feeding upon this species. In laboratory feeding trials, *P. audax* always retreated from *C. pennsylvanicus* and always attacked *D. undecimpunctata.* Also, *P. audax* retreated from models displaying the markings of *C. pennsylvanicus* in 88% and attacked models displaying the markings of *D. undecimpunctata* in 85% of the laboratory trials.

Jumping spiders (Salticidae) are diurnal stalking predators (Foelix 1979; Forster 1985) which may select prey from many insects and spiders (Snetsinger 1955; Foelix 1979; Forster 1985; Jackson 1992; Edwards & Jackson 1993). Several studies have suggested that *Phidippus audax* (Hentz 1845), a large and widely distributed salticid, favors Diptera as prey but will also take slow-moving caterpillars and beetles (Freed 1984; Forster 1985; Edwards & Jackson 1993). Beetles may be very common in habitats containing *P. audax*; however, there is little information on the interaction of *P. audax* with these insects. Givens (1978) suggested that *P. audax* avoided adult dermestid beetles because the hard dorsal prothoracic shield was impenetrable to the jaws of the spider. Not only do many beetles have very hard prothoracic shields and wing covers but also many beetles possess noxious defensive compounds (Blum 1981; Harborne 1993). As a result, Coleoptera are often avoided by spiders (Reichert & Harp 1987). Despite the general avoidance of beetles, certain species are taken as prey. In separate studies of the foraging behavior of *P. audax* by Edwards (1980) and Freed (1984), spiders took both *Chauliognathus* and *Disonycha* (Alticinae, Chrysomelidae) as prey.

In the tallgrass prairie of northeastern Kansas, *P. audax* is a common species which is frequently encountered in moist lowlands (Fitch 1963; pers. obs.). In this habitat, two species of soft-bodied beetles, *Chauliognathus pennsylvanicus* and *Diabrotica undecimpunctata* are also common. The purpose of this study was to 1) estimate the density of *P. audax*, *C. pennsylvanicus*, and *D. undecimpunctata* in these lowlands, 2) determine the use of common soft-bodied prey species by *P. audax*, and 3) quantify how *P. audax* interacts with *C. pennsylvanicus* and *D. undecimpunctata.* Furthermore, a comparison of observed responses to prey species in the field with laboratory feeding trials and responses to models may shed light on salticid-coleopteran interactions in tallgrass prairie wetlands and the role of salticids in prairie spider assemblages (Robinson 1984).

METHODS

The field portion of this study was conducted in the lowland portions of two annually burned and two biennially burned watersheds on the Konza Prairie Research Natural Area (KPRNA) located approximately 15 km south of the town of Manhattan, Kansas. In these watersheds, upland plant communities are dominated by big bluestem, *Andropogon gerardii*, and Indian grass, *Sorghastrum nutans*. Lowland plant communities are dominated by prairie cordgrass, *Spartina pectinata*, and switchgrass, *Panicum virgatum*. Common forbs in both upland and lowland communities are the common milkweed (*Asclepias*

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syriaca), tall thistle (*Cirsium altissimum)* and Baldwin's ironweed (*Vernonia baldwinii).*

In order to obtain a crude estimate of the average density of actively hunting *P. audax* in the field, I counted the numbers of spiders found on leaves of *A. syriaca*, *C. altissimum* and *V. baldwinii* along three parallel 25 m transects that ran through each lowland site. The densities of these three plants in the lowlands were estimated by taking 30 quadrat samples, each 0.1 m^2, in the lowland sites (Johnson & Knapp 1995). I estimated the densities of *C. pennsylvanicus* and *D. undecimpunctata* using the same method supplemented by shaking the entire contents of inflorescences and upper leaves into a sweep net, then freezing and counting the number of insects collected. Because I was simultaneously observing spider behavior, I chose not to take sweep samples of common milkweed and tall thistle foliage so that the spiders would not be disturbed.

Observations were made between 1000–1600 h every other day from mid-July to late October 1992. At the beginning of this period, all *Phidippus audax* were large juveniles approximately 13–15 mm in body length. Length of spiders was obtained by measuring seven individuals which had been killed in ethyl acetate. I recorded the plant species on which these spiders were found, their positions on the plant, and whether or not they were engaged in feeding. If they were feeding, the type of prey they were feeding upon was recorded.

Laboratory feeding trials.—Five late instar juvenile *P. audax* were collected from the campus of Kansas State University (Manhattan) in early August 1992, when spiders were approximately 15 mm long. These spiders were kept and tested in 20 cm × 15 cm × 8 cm clear plastic boxes. Each box was fitted with an open, mesh covered top to maintain good internal air circulation. Distilled water was sprayed into the containers every other day to simulate morning dew or light rainfall. Containers were illuminated on a 16:8 h light:dark cycle with four fluorescent lights and two incandescent lights all supplemented with sunlight from a north-facing window. This provided a minimum illumination of 350 lx.

In order to clarify the interactions between *Phidippus audax* and *Diabrotica undecimpunctata* and *Chauliognathus pennsylvanicus* observed in the field, I collected these beetles from the field and introduced them to the spiders' containers. Either of the beetle species was given to spiders every five days in no repeating order. Once a beetle was placed inside the test chamber, responses were observed over a 15 min period and categorized as either an attack or a retreat (see Jackson & Olphen 1992). Response data were analyzed using a Kruskal-Wallis non-parametric repeated measures analysis of variance in SAS at an $\alpha = 0.5$ (Zar 1984; SAS Institute 1988).

Responses to models.—To further investigate how *P. audax* interacts with *C. pennsylvanicus* and *D. undecimpunctata*, models were made of both beetles. These models were made from 10 cm wide × 1.5 mm thick plastic sheets that were cut to the approximate length and width of *C. pennsylvanicus* (5 mm × 14 mm) and *D. undecimpunctata* (5 mm × 8.5 mm). The models were then painted to match the color and spot patterning of each beetle. Alternate sized models were also made of both types of spot patterning (*C. pennsylvanicus* size with *D. undecimpunctata* patterning and *vice versa*) to test the effects of size on spider response. Models were designed primarily to represent dorsal surfaces of the beetles. The models were manipulated outside of the spiders' containers which allowed free movement of the model and a clear view of the model to the spider without opening the spiders' containers (Fig. 1). Each model was mounted onto a 30 cm length of wire and manipulated by hand so that the path taken by the model could change direction and speed (approximately 1–10 mm/s). This speed range was based on observed behavior of beetles in the field and in the lab. The 30 cm length of wire allowed easy manipulation of the model while also greatly reducing observer effects on spider responses by keeping the manipulator's hand beyond the visual range of the spider. Both models were presented to each spider 30 times in no repeating order. Therefore, each spider was involved in a total of 120 interactions (30 trials/spider × 4 models) and each model was used 150 times (30 trials/spider × 5 spiders).

So that spiders might be interested in food but not starved, no spider-model trials were conducted within two and no later than four days following a feeding. Spider responses to models were recorded in a manner similar to that of the responses to live prey species. Response data were analyzed in the same way as the data from the feeding trial experiment.

RESULTS AND DISCUSSION

Throughout the field study, *Phidippus audax* was observed primarily on *Asclepias syriaca* (79%

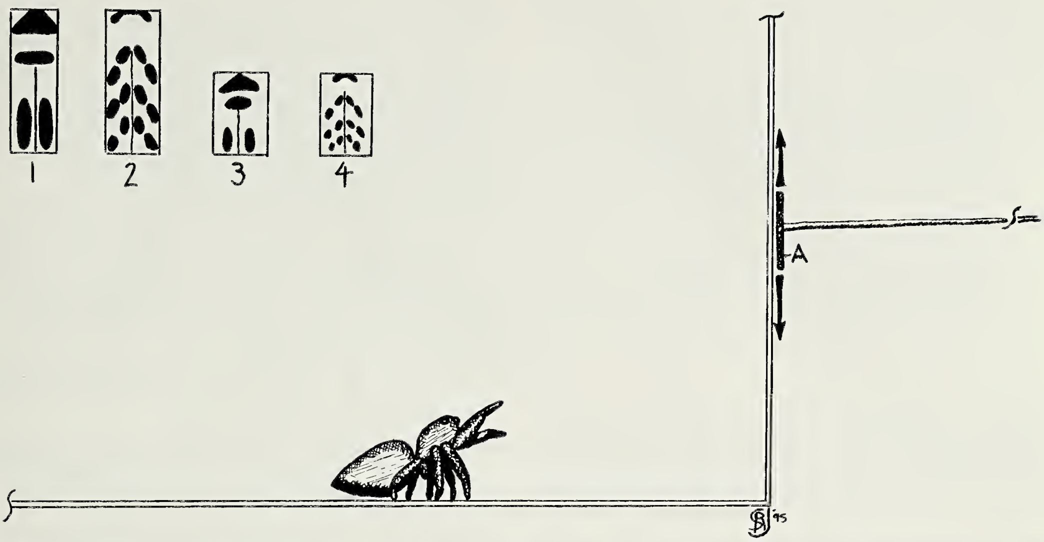

Figure 1.—Arrangement of test chamber and position of model (A) relative to spider. Appearance of models is shown in upper left corner. 1, *Chauliognathus pennsylvanicus* normal size (ChN); 2, *Diabrotica undecimpunctata* large size (DiL); 3, *C. pennsylvanicus* small size (ChS); and 4, *D. undecimpunctata* normal size (DiN).

of all observations, $n = 45$) or *Cirsium altissimum* (21% of all observations) with an estimated density of 3.2 ± 0.5 spiders/m^2. Estimated densities of *D. undecimpunctata* were 10.9 ± 1.8 beetles/m^2 and 20.3 ± 5.2 beetles/m^2, for *C. pennsylvanicus*. Both beetles were most concentrated on *C. altissimum* and *V. baldwinii* (Fig. 2). From late September–late October, estimated densities of *P. audax* and both beetles were lower (Fig. 2).

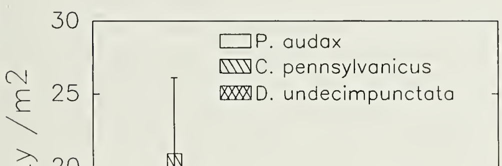

Figure 2.—Estimated density of *Phidippus audax*, *Diabrotica undecimpunctata* and *Chauliognathus pennsylvanicus* in lowlands on Konza Prairie Research Natural Area from mid-summer to mid-autumn, 1992. Vertical bars indicate one standard error of the mean for 12 transects.

In a total of 25 field observations of spiders with prey, *P. audax* was most often found feeding upon *Archytas* sp. (Diptera, Tachinidae) (75% of observations) or upon *D. undecimpunctata* (15% of observations). In the remaining 10% of observations, *P. audax* was feeding upon small moths (unidentified), juvenile grasshoppers (unidentified), *Tetragnatha laboriosa* (Araneae, Araneidae), *Hibana gracilis* (Araneae, Anyphenidae), juvenile *Araneus* sp. or gnaphosid spiders.

Laboratory feeding trials.—In the laboratory feeding trials, all *P. audax* attacked and ate *D. undecimpunctata* in 100% of feeding trials. Conversely, interactions between *P. audax* and *C. pennsylvanicus* involved either no response or actual retreat by the spiders in 100% of the trials.

Responses to prey models.—In the model presentation experiments, there was no significant difference in response to models based on size alone ($F_{0.05,1,1} = 2.08$, $P > 0.1$); however, the differences in response were significant when based on pattern alone ($F_{0.05,1,1} = 47.51$, $P < 0.01$). The normal sized model of *C. pennsylvanicus* elicited retreat behavior in 88 ± 2% of the trials while the small model elicited retreat behavior in 80 ± 3% of the trials. There was no significant difference between the number of attack and retreat responses to the large model of

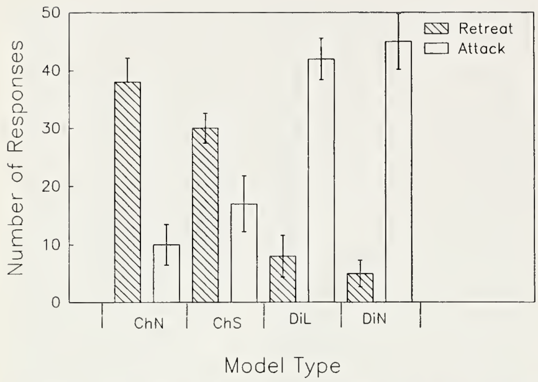

Figure 3.—Number and type of response elicited in *Phidippus audax* by the normal (ChN) and small (ChS) models of *Chauliognathus pennsylvanicus* and the large (DiL) and normal (DiN) sized models of *Diabrotica undecimpunctata*. Vertical bars indicate one standard error of the mean for 150 trials.

D. undecimpunctata while the normal sized model of *D. undecimpunctata* elicited attack behavior in the spiders in 85 ± 2% of the trials (Fig. 3). Therefore, the avoidance response of *P. audax* to the models of *C. pennsylvanicus* was more related to the species spot patterns than to size.

The responses of these spiders indicate that in northeastern Kansas they may actively avoid *C. pennsylvanicus*. This may be a regional difference in response since *P. audax* from Florida, as observed by Edwards (1980) and Freed (1984), did take the congener *C. maginatus* as prey. *Chauliognathus pennsylvanicus* may have been avoided by the *P. audax* in this study because of regional differences in the toxicity of the beetles, or because the beetles were different species.

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EFFECTS OF CULTURAL PRACTICES ON THE SPIDER (ARANEAE) FAUNA OF LOWBUSH BLUEBERRY FIELDS IN WASHINGTON COUNTY, MAINE

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ABSTRACT. Spiders of 17 families, 53 genera, and 87 species were captured in pitfall traps (n = 45 traps/year) placed in lowbush blueberry fields in Washington County, Maine, during the summers of 1986 and 1987. Species and numbers of hunting spiders (Lycosidae, Gnaphosidae, Thomisidae) were numerically dominant. Significantly more (ANOVA, G-tests) spiders were captured in 1987 than in 1986. Sex ratios were highly biased toward males both years. Species richness, diversity, and evenness of trapped spiders varied among three blueberry cultural treatments (mowing, burning, bearing crop). In 1986, richness and diversity were greatest in crop bearing fields, with spiders more evenly distributed in burned fields. In 1987, species richness, diversity, and evenness were greatest in burned fields. Over all weeks in 1986, there were no significant differences (ANOVA, DMRT) in mean numbers of individuals or species captured among treatments. Significant differences in mean catches among treatments were observed on one of nine sampling dates in 1986. Greater variatión was seen in 1987 for both individuals and species; significant differences in mean catches among treatments were noted on six of 12 sampling dates. Percentage similarity (PS) of species quantities among treatments was > 60; PS values were greater in 1986 than in 1987. The blueberry-spider fauna had more species in common (QS) with terrestrial habitats than arboreal habitats in Maine.

Lowbush blueberry, *Vaccinium angustifolium* (Ait.), is a perennial shrub native to northeastern North America (Vander Kloet 1978). In Maine, lowbush blueberry is fostered and nurtured for berry production; it comprises a major commercial crop. Numerous cultural practices have been developed and implemented to promote berry production. These practices include: herbicidal control of competing weeds; insecticidal control of pestiferous insects; irrigation of fields during periods of drought; and artificial pruning of older plants by either burning or mowing. Recently, mowing blueberry fields has evolved as an alternative management practice to burning. Since early times, burning blueberry fields was the method used not only to prune blueberry plants, but also to suppress competing vegetation. However, the long-term effects of burning, mowing, or other cultural practices have not been fully evaluated for the blueberry agroecosystem.

In Arkansas, Johnson et al. (1981) and Hopkins & Johnson (1984) reported that spider populations were higher and somewhat more diverse in wild blueberries (*Vaccinium* spp.) than in cultivated, highbush blueberries (*V. corymbosum* L.). However, in Maine the arthropod fauna associated with blueberry plants and with blueberry fields has received scant attention; most studies concern only pest insects (Forsythe & Collins 1986, 1987, 1988). We know of no previous studies concerning the possible effects of either burning or mowing on the araneofauna associated with lowbush blueberry in Maine.

Some information is available about the effects of burning and mowing on spider populations in other ecosystems. Most studies have shown that spider numbers decline following burning (Riechert & Reeder 1972; Nagel 1973; Dunwiddie 1991); however, Aitchison-Benell (1994) found that numbers of bog spiders were high two months after fire and then decreased. Other investigations have shown that spider numbers also decline after mowing (Howell & Pienkowski 1971; Nyffeler & Breene 1990; Dunwiddie 1991).

In this paper, we: 1) describe the araneofauna associated with lowbush blueberry fields in commercial production in Washington County, Maine; 2) compare the density of pitfall-trap catches among three blueberry cultural treatments (pruning by mowing = "mow", pruning by burning = "burn", and bearing crop = "bear"); 3) evaluate the effects of these three cultural treatments on spider species composition and abundance; and 4) compare the terricolous spider fauna of Maine's blueberry fields with that of other habitats.

METHODS

Study sites.—Commercial lowbush blueberry fields that represented three blueberry cultural treatments (mow, burn, bear) were sampled for spiders in Washington County, Maine in 1986 and 1987. Three fields were selected and monitored for each treatment each year.

Treatments.—Burn treatments were applied in November prior to each study year, i.e., 1985 or 1986. Mow treatments were applied in April of each study year, i.e., 1986 or 1987. Mow treatment areas were flail-mowed by the grower using standard commercial flail-mowers. Burn treatment areas were similarly burned with commercial oil burners by the grower. Hexazinone (herbicide) and fertilizer were applied to mow and burn fields by the grower following standard lowbush blueberry management practices (University of Maine Cooperative Extension Service 1986). In 1986, phosmet (insecticide) was applied to one bear field between 4–11 July; in 1987, azinphos-methyl (insecticide) was applied to one bear field between 10–17 July. Both insecticide treatments were standard applications to control blueberry maggot, *Rhagoletis mendax* Curran.

Pitfall traps.—At each study site, we deployed five pitfall traps along line transects; starting points and orientations of transects were chosen at random and were at least 20 m from field edges and roads. Pitfall traps were 0.5 liter plastic drinking cups (height, 13.0 cm; top diameter, 8.6 cm). Each cup was filled to a depth of about 5 cm with ethylene glycol (antifreeze). A rain cover (12.7 × 12.7 cm) constructed of 0.6 cm exterior plywood, and with four 16d nails (length = 8.9 cm) as supports, was placed over each trap and remained in place until the traps were serviced.

In 1986, traps were deployed on 20 June and serviced weekly until 22 August for a total of nine trap weeks. In 1987, traps were deployed on 15 May and serviced weekly until 14 August for a total of 12 trap weeks. At each servicing, traps were removed from the ground and their contents passed through a fine mesh strainer. Captured organisms were placed in small jars with 70% ethanol and transported to the laboratory for sorting and identification of spiders. Potential sample sizes were: n = 45 traps/year; 5 traps/field × 3 cultural treatments × 3 replications/treatment × 9 weeks = 405 in 1986, and × 12 weeks = 540 in 1987.

Spider identifications.—Only sexually mature spiders were identified to species; species determinations follow the identification keys and descriptions of Kaston (1981). Juveniles, including penultimate stages, were identified to genus. A few specimens (mostly Linyphiidae) were sent to Dr. C. D. Dondale, Ottawa, for species determination or confirmation. Representative specimens of all identified species will be deposited in the arachnid collection, U. S. National Museum of Natural History, Washington, DC.

Data analyses.—*Spider taxa:* We used nonparametric procedures (Sokal & Rohlf 1981) for statistical comparisons at $P = 0.05$. The G-test was used to compare spider abundances between years and by foraging strategy, and to compare sex ratios of trapped males and females. Null hypotheses were: expected abundances equal between years; expected abundances equal between foraging strategies (web spinner, hunter); and expected proportions (0.50: 0.50) of spider sexes.

Data analyses.—*Species richness, diversity, and evenness:* Computations of species richness, diversity, and evenness were made using the program of Ludwig & Reynolds (1988), where: species richness, NO = the number of *all* species in the sample regardless of their abundances (Hill 1973); species diversity, H' = Shannon's index (Shannon & Weaver 1949); and species evenness, $E5$ = a measure of how evenly species are distributed in a sample. For species comparisons, we included only those species represented by adult spiders; hence, our estimates are conservative.

For comparisons of species similarities

among blueberry cultural treatments (*Q*-mode analysis), we used the percent similarity (*PS*) index of Bray & Curtis (1957), which takes into account species quantities in sampling units.

Sørensen's similarity quotient (*QS*), as defined by Price (1975), was used to compare the terricolous spider fauna we found in blueberry fields of Maine with that of other similar and dissimilar habitats in Maine. For these comparisons, we excluded species identified only to genus in the various studies. Hence, our estimates of spider faunal similarities in Maine may be conservative.

Data analyses.—*Treatment effects:* Parametric procedures were used to evaluate treatment effects. Prior to analysis, pitfall-catch data were subjected to Hartley's test for homogeneity of variance (Sokal & Rohlf 1981). Log transformations ($\log_{10}(X + 1)$) were used to stabilize variances. Analysis of variance (ANOVA) ($P = 0.05$) and Duncan's Multiple Range Test (DMRT) ($\alpha = 0.05$) (SAS Institute 1985) were used to evaluate differences in mean catches of individuals and species among treatments by week and over all weeks for each year.

RESULTS

Spider taxa.—Spiders of 17 families, 53 genera, and 87 species were pitfall-trapped in blueberry fields of Washington County, Maine during the summers of 1986 and 1987 (Table 1). Except for number of families, fewer taxa were trapped in 1986 than in 1987: 15 families, 38 genera, 54 species in 1986; 15 families, 44 genera, and 73 species in 1987. Four of the species trapped in 1986 were represented by juveniles only. Species of Araneidae and Anyphaenidae were trapped in 1986 but not in 1987; species of Hahniidae and Tetragnathidae were trapped in 1987 but not in 1986.

For both study years, species composition of spiders differed by foraging strategy; species of hunters were numerically dominant (Fig. 1). In 1986, the hunter guild was comprised mainly of species of Lycosidae (20.4% of all species), Gnaphosidae (14.8%), and Thomisidae (11.1%); collectively, the remaining hunter families comprised 27.8% of the total species ($n = 54$). In 1987, the hunter guild consisted of species of Lycosidae (21.9%), Gnaphosidae (16.4%), and Thomisidae (13.7%); collectively, the remaining hunter families comprised 20.6% of the total species ($n = 73$) trapped that year.

Numbers of individuals also differed by foraging strategy each year; individuals of the hunter guild were by far the most commonly trapped spiders each year and for both years combined (Fig. 2). In 1986, the hunter guild consisted chiefly of individuals of Lycosidae (72.2% of all individuals), Gnaphosidae (6.8%), and Thomisidae (8.8%); collectively, the remaining hunter families comprised 6.7% of the total trapped individuals ($n = 832$). Again, in 1987 the Lycosidae were numerically dominant (77.8% of all trapped individuals), followed by the Gnaphosidae (7.0%) and the Thomisidae (6.5%). Collectively, the remaining hunter families comprised 4.2% of the total trapped individuals ($n = 1{,}890$).

Spider numbers, life stages, sex ratios.—The pitfall traps yielded a total of 2,722 spiders; 832 (30.6% of all individuals) were trapped in 1986, and 1,890 (69.4% of all individuals) were trapped in 1987 (Table 1). Significantly more spiders were trapped in 1987 than in 1986; likewise, more web spinners and more hunters were trapped in 1987 than in 1986 (Table 1). *G*-tests also indicated that significantly more adult spiders of 13 species and juveniles of two genera (i.e., *Callobius* sp., *Pardosa* spp.) were trapped in 1987 than in 1986. However, adults of only one species (*Pirata minutus* Em.) and juveniles of two genera (*Alopecosa* sp., *Xysticus* sp.) had significantly more spiders trapped in 1986 than in 1987 (Table 1).

For both study years, males were the most prevalent life stage trapped, followed by juveniles and females: 54.6% males, 26.4% juveniles, 19.0% females in 1986; and 62.0% males, 19.3% juveniles, 18.8% females in 1987. Sex ratios of males to females were highly biased toward males both years: ratio 2.9:1, $G = 149.3$, $P < 0.001$ in 1986; and ratio 3.3:1, $G = 460.0$, $P < 0.001$ in 1987.

Species richness, diversity, evenness.—Species richness, diversity, and evenness varied among treatments within years, among treatments between years, and over all treatments between study years (Table 2). In 1986, richness and diversity were greatest in the bear fields; however, spiders were distributed more evenly among species in the burn fields. For the last nine weeks of trapping in 1987, species richness was greatest in the bear

Table 1.—Species and numbers of spiders captured in pitfall traps in blueberry fields of Washington County, Maine, 1986 and 1987 (n = 45 traps/year; 5 traps/field × 3 cultural treatments × 3 replications/treatment). G-test of spider abundance between years; significance levels: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. MO = Mow, BU = Burn, BE = Bear.

	1986 (9 weeks)			1987 (12 weeks)			
	MO	BU	BE	MO	BU	BE	*G*
WEB SPINNERS							
Theridiidae							
Achaearanea globosa (Hentz)	1	0	0	0	0	0	
Enoplognatha marmorata (Hentz)	5	4	15	8	14	9	0.89
Enoplognatha sp.	0	0	0	1	1	1	
Euryopis saukea Levi	0	0	1	0	0	0	
Robertus spiniferus (Em.)	1	0	0	0	1	0	
Linyphiidae							
Subfamily Linyphiinae							
Bathyphantes pallidus (Banks)	1	0	1	0	0	7	2.94
Lepthyphantes calcarata (Em.)	0	0	0	0	0	1	
Meioneta fabra (Keys.)	2	0	0	1	1	0	
Meioneta simplex (Em.)	0	0	0	1	0	0	
Microlinyphia mandibulata (Em.)	0	0	0	0	1	1	
Neriene clathrata (Sundv.)	0	0	0	0	0	1	
Oreonetides sp. 1	0	0	0	1	0	0	
Subfamily Erigoninae							
Baryphyma longitarsum (Em.)	0	0	0	1	0	0	
Collinsia plumosus (Em.)	0	0	1	0	0	0	
Grammonota angusta Dondale	0	0	2	1	1	1	0.20
Grammonota capitata Em.	0	0	0	2	0	0	
Pocadicnemis americana Mill.	0	0	0	0	0	2	
Undet. sp.	0	0	0	0	1	1	
Tetragnathidae							
Pachygnatha tristriata C. L. Koch	0	0	0	0	0	1	
Araneidae							
Araneus trifolium (Hentz)	0	1	0	0	0	0	
Neoscona arabesca (Walck.)	1	0	0	0	0	0	
Agelenidae							
Agelenopsis actuosa (Gertsch & Ivie)	1	3	0	0	1	0	1.93
Agelenopsis utahana (Chamb. & Ivie)	0	0	0	1	0	0	
Hahniidae							
Neoantistea agilis (Keys.)	0	0	0	0	1	0	
Dictynidae							
Argenna obesca Em.	1	0	0	0	0	0	
Cicurina pallida Keys.	0	0	0	0	1	0	
Cicurina placida Banks	0	0	0	0	1	1	
Cicurina sp.	1	0	0	0	1	0	
Amaurobiidae							
Callobius bennetti (Blkw.)	0	0	0	5	1	0	
Callobius sp.	0	1	2	8	2	0	3.98*
Webspinner subtotals	14	9	22	30	28	26	11.98***
HUNTERS							
Lycosidae							
Alopecosa aculeata (Clerck)	2	2	3	17	38	20	65.84***

Table 1.—Continued.

	1986 (9 weeks)			1987 (12 weeks)			
	MO	BU	BE	MO	BU	BE	*G*
Alopecosa kochi (Keys.)	0	0	0	4	4	2	
Alopecosa sp.	4	6	6	1	2	0	9.77**
Hogna frondicola (Em.)	0	0	3	4	5	6	8.73**
Hogna sp.	10	9	7	12	23	2	1.93
Pardosa distincta (Blkw.)	68	53	57	98	22	96	3.67
Pardosa fuscula (Thor.)	0	0	0	0	1	0	
Pardosa hyperborea (Thor.)	0	1	0	0	3	1	1.93
Pardosa milvina (Hentz)	0	0	0	1	2	0	
Pardosa moesta Banks	29	22	10	50	81	238	244.95***
Pardosa saxatilis (Hentz)	7	5	4	7	34	53	61.25***
Pardosa xerampelina (Keys.)	0	2	1	6	65	37	126.30***
Pardosa spp.	7	5	6	37	39	40	80.03***
Pirata insularis Em.	0	0	0	1	0	0	
Pirata minutus Em.	7	17	12	3	4	10	6.96**
Pirata sp.	0	1	1	1	1	1	0.20
Schizocosa communis (Em.)	46	41	34	73	92	79	42.27***
Schizocosa crassipalpata Roewer	0	0	1	0	1	2	1.05
Schizocosa saltatrix (Hentz)	0	0	0	0	0	1	
Schizocosa sp.	0	0	0	3	10	3	
Trochosa terricola Thor.	0	0	1	1	1	4	3.96*
Trochosa sp.	0	0	2	3	2	0	1.33
Undet. sp.	59	0	50	4	7	113	0.97
Anyphaenidae							
Wulfila saltabundus (Hentz)	0	0	1	0	0	0	
Liocranidae							
Agroeca ornata Banks	0	0	0	1	0	0	
Agroeca sp.	0	0	1	0	0	0	
Phrurotimpus alarius (Hentz)	1	0	0	0	0	0	
Phrurotimpus borealis (Em.)	1	1	0	1	0	0	0.34
Scotinella divesta (Gertsch)	0	0	0	0	0	1	
Clubionidae							
Clubiona bishopi Edwards	1	0	0	0	0	0	
Clubiona johnsoni Gertsch	1	2	1	6	4	5	6.78**
Clubiona kastoni Gertsch	0	1	0	0	0	0	
Clubiona sp.	1	0	0	1	2	1	1.93
Corinnidae							
Castianeira cingulata (C. L. Koch)	0	4	0	0	0	0	
Castianeira descripta (Hentz)	4	6	8	1	6	6	0.81
Castianeira sp.	2	1	4	0	2	0	2.94
Gnaphosidae							
Drassodes neglectus (Keys.)	0	0	0	2	1	1	
Drassyllus depressus (Em.)	1	0	0	0	1	0	
Drassyllus socius Chamb.	0	0	0	0	2	0	
Gnaphosa muscorum (L. Koch)	5	1	5	0	6	0	1.49
Gnaphosa parvula Banks	2	1	2	5	5	6	6.06*
Gnaphosa sp.	1	2	2	1	5	4	1.70
Haplodrassus bicornis (Em.)	0	0	0	5	4	7	
Haplodrassus hiemalis (Em.)	0	0	0	0	1	1	
Haplodrassus signifer (C. L. Koch)	0	3	5	18	12	10	23.29***
Haplodrassus sp.	0	1	1	2	1	2	1.33

Table 1.—Continued.

	1986 (9 weeks)			1987 (12 weeks)			
	MO	BU	BE	MO	BU	BE	*G*
Herpyllus ecclesiasticus Hentz	0	0	0	1	0	0	
Micaria riggsi Gertsch	0	0	2	1	4	1	2.09
Sergiolus decoratus Kaston	1	0	0	0	0	0	
Zelotes fratris Chamb.	0	2	0	2	0	1	0.20
Zelotes hentzi Barrows	3	1	11	6	2	6	0.03
Zelotes sp.	2	1	2	2	1	4	0.33
Philodromidae							
Ebo iviei Sauer & Platnick	0	0	0	1	0	0	
Philodromus placidus Banks	0	0	0	0	1	0	
Philodromus sp.	0	0	0	0	1	0	
Thanatus formicinus (Clerck)	0	0	0	1	1	0	
Thanatus striatus C. L. Koch	0	0	0	0	1	0	
Thanatus sp.	2	0	0	1	2	0	0.20
Thomisidae							
Coriarachne utahensis (Gertsch)	0	0	0	3	0	0	
Ozyptila distans Dondale & Redner	0	0	1	0	0	1	
Ozyptila sp.	0	0	0	1	0	0	
Xysticus alboniger Turnbull, Dondale & Redner	2	0	1	0	1	3	0.14
Xysticus ampullatus Turnbull, Dondale & Redner	2	3	3	8	2	25	18.29***
Xysticus discursans Keys.	0	0	1	3	3	7	12.20***
Xysticus emertoni Keys.	0	0	0	1	2	4	
Xysticus ferox (Hentz)	0	0	0	2	0	7	
Xysticus fervidus Gertsch	0	0	0	0	1	0	
Xysticus pellax O. P.-Camb.	0	0	1	0	0	0	
Xysticus triguttatus Keys.	7	12	22	9	20	13	0.01
Xysticus winnipegensis Turnbull, Dondale & Redner	0	0	0	0	0	1	
Xysticus spp.	6	6	6	1	1	4	6.28*
Salticidae							
Euophrys monadnock Em.	0	0	2	1	1	0	
Evarcha hoyi (Peckham & Peckham)	1	0	0	0	0	0	
Habronattus decorus (Blkw.)	0	1	0	0	1	0	
Habronattus viridipes (Hentz)	3	2	0	9	8	4	10.59**
Habronattus sp.	1	0	0	1	1	0	0.34
Phidippus purpuratus Keys.	0	0	2	0	2	0	
Phidippus whitmani Peckham & Peckham	0	0	0	0	0	1	
Phidippus sp.	1	0	0	1	0	2	1.05
Talavera minuta (Em.)	0	0	0	0	0	1	
Hunter subtotals	290	215	282	424	545	837	411.45***
Spider Totals	304	224	304	454	573	863	422.26***

fields; however, diversity and evenness were greatest in burn fields (Table 2). Over 12 weeks in 1987, species richness, diversity, and evenness were greatest in the burn fields, followed by bear fields for richness, and mow fields for diversity and evenness. And, over all treatments, species richness, diversity, and evenness generally were greater in 1987 than

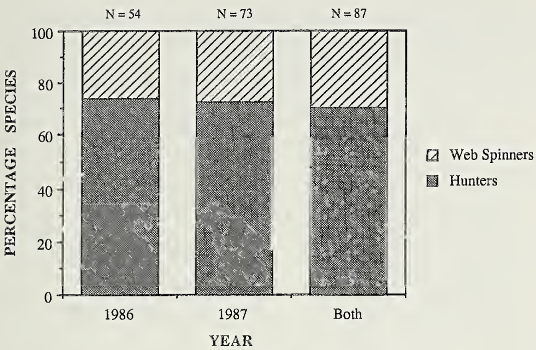

Figure 1.—Percentages of spider species, by foraging strategy (web-spinner, hunter), captured in pitfall traps, blueberry fields, Washington County, Maine; 9 weeks, 1986; 12 weeks, 1987; and both years combined.

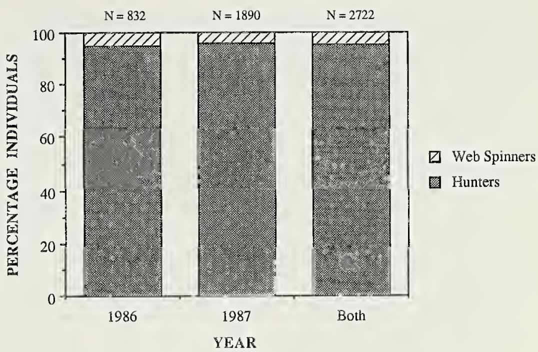

Figure 2.—Percentages of spider individuals, by foraging strategy (web-spinner, hunter), captured in pitfall traps, blueberry fields, Washington County, Maine; 9 weeks, 1986; 12 weeks, 1987; and both years combined.

in 1986 (Table 2). For both study years combined and over all treatments, the computed values were: NO = 87, H' = 2.77, $E5$ = 0.52.

The ranking order of species abundance for the 10 most commonly trapped species also differed between study years (Table 3). Because of their common occurrence in trap catches, *Pardosa distincta, P. moesta*, and *Schizocosa communis* were among the three top-ranked species each study year and for both years combined. The dominance of the hunter guild was very evident in the rank order of species abundance; for each year and both years combined, fully 90% were hunters with only one web-spinner species, *Enoplognatha marmorata* (Hentz), included among the rankings.

Mean numbers of individuals and species.—Over all weeks in 1986, there was no significant difference in mean numbers of individuals (ANOVA, F = 0.78, df = 42) trapped (Table 4). In 1987, significantly more individuals were captured in the bear fields than in either the mow or burn fields (ANOVA, F = 8.00, df = 42). Although mean numbers of species trapped in 1986 did not differ significantly (ANOVA, F = 0.85, df = 42), both bear and burn fields had significantly more species than mow fields (ANOVA, F = 9.02, df = 42) in 1987. To minimize temporal variation and equalize sample sizes, we excluded the first three weeks of trapping in 1987 and reanalyzed the data. As expected, mean catches of individuals and species were slightly lower for nine weeks of trapping in 1987. However, all test comparisons remained the same, except mean catches of species in burn fields did not differ significantly from

Table 2.—A comparison of spider species richness, diversity, and evenness among three blueberry cultural treatments, Washington County, Maine, 1986, 1987 (NO = number of all species; H' = Shannon diversity index; $E5$ = evenness index; all from BASIC program SPDIVERS.BAS (Ludwig & Reynolds 1988)).

	1986 (9 weeks)				1987 (9 weeks)				1987 (12 weeks)			
	Mow	Burn	Bear	All	Mow	Burn	Bear	All	Mow	Burn	Bear	All
Richness												
NO	29	25	31	50	33	35	38	59	43	49	44	73
Diversity												
H'	2.26	2.34	2.59	2.54	2.22	2.51	2.32	2.51	2.63	2.74	2.44	2.73
Evenness												
E5	0.54	0.61	0.59	0.51	0.51	0.56	0.50	0.53	0.51	0.59	0.48	0.52

Table 3.—Ranking order of abundance for the 10 most commonly trapped terricolous spiders in blueberry fields of Washington County, Maine, 1986 and 1987, and both years combined.

1986 (9 weeks)	1987 (9 weeks)	1987 (12 weeks)	Both years
1. *Pardosa distincta*	*Pardosa moesta*	*Pardosa moesta*	*Pardosa moesta*
2. *Schizocosa communis*	*Schizocosa communis*	*Schizocosa communis*	*Pardosa distincta*
3. *Pardosa moesta*	*Pardosa distincta*	*Pardosa distincta*	*Schizocosa communis*
4. *Xysticus triguttatus*	*Pardosa saxatilis*	*Pardosa xerampelina*	*Pardosa xerampelina*
5. *Pirata minutus*	*Pardosa xerampelina*	*Pardosa saxatilis*	*Pardosa saxatilis*
6. *Enoplognatha marmorata*	*Enoplognatha marmorata*	*Alopecosa aculeata*	*Xysticus triguttatus*
7. *Castianeira descripta*	*Xysticus triguttatus*	*Xysticus triguttatus*	*Alopecosa aculeata*
8. *Pardosa saxatilis*	*Alopecosa aculeata*	*Haplodrassus signifer*	*Enoplognatha marmorata*
9. *Zelotes hentzi*	*Pirata minutus*	*Xysticus ampullatus*	*Pirata minutus*
10. *Gnaphosa muscorum*	*Gnaphosa parvula* *Habronattus viridipes*	*Enoplognatha marmorata*	*Haplodrassus signifer*

mean catches in either mow or bear fields (Table 4).

Summaries of mean numbers of individuals and species of spiders captured in pitfall traps by sampling week are shown in Figs. 3 and 4, respectively. In 1986, the only significant difference in mean number of individuals occurred on 18 July (ANOVA, $F = 4.01$, $df = 42$) (mow > bear). Peaks in mean number of individuals on 25 July (bear) and 8 August (mow) were due to large numbers of spiderlings captured in one trap on each date ($n = 50$ and 57, respectively). Much greater variation between and among cultural treatments was observed in 1987. Bear fields had significantly more individuals than mow fields on 22 May and 7 August (ANOVA, $F = 4.11$ and 5.04, respectively, $df = 42$) and significantly more individuals than either burn or mow fields on 5, 12, and 19 June (ANOVA, $F = 6.42$, 5.63, and 9.34, respectively, $df = 42$) (Fig. 3). Significantly more individuals were captured in burn fields than mow fields on 29 May (ANOVA, $F = 3.94$, $df = 42$). The large peak in mean numbers of individuals captured in bear fields on 7 August was due to large numbers of spiderlings ($n = 44$ and 66) in two traps.

In 1986, significantly more species were found in mow fields compared to bear fields on 18 July (ANOVA, $F = 2.82$, $df = 42$). Similar variations were observed in mean numbers of species trapped in 1987 (Fig. 4). Significantly more species were trapped in bear than in mow fields on 22 May, 5 June, 19 June, and 7 August (ANOVA, $F = 4.51$, 3.25, 5.14, and 5.11, respectively, $df = 42$). Bear fields had significantly more species than either mow or burn on 12 June (ANOVA, $F = 5.26$, $df = 42$); burn fields had significantly more species than mow on 29 May (ANOVA, $F = 3.60$, $df = 42$).

In 1986, mean numbers of individuals and species generally declined in all fields after 4

Table 4.—Comparison of mean individuals and species of spiders associated with three blueberry cultural treatments. Column means followed by the same letter are not significantly different ($P = 0.05$); ANOVA and DMRT. Log transformations, $\log_{10}(X + 1)$, were used to stabilize variances. Sample sizes were: 15 traps/treatment × 9 weeks = 135, 1986 and 1987; 15 traps/treatment × 12 weeks = 180, 1987.

	X (±SE) individuals			X (±SE) species		
Field condition	1986 (9 weeks)	1987 (9 weeks)	1987 (12 weeks)	1986 (9 weeks)	1987 (9 weeks)	1987 (12 weeks)
MOW	2.25a (0.43)	2.45b (0.40)	2.52b (0.36)	0.99a (0.10)	1.41b (0.20)	1.47b (0.18)
BURN	1.66a (0.23)	2.62b (0.28)	3.18b (0.26)	1.04a (0.12)	1.64ab (0.15)	1.89a (0.11)
BEAR	2.25a (0.51)	4.26a (0.71)	4.79a (0.61)	1.23a (0.15)	2.01a (0.12)	2.32a (0.13)

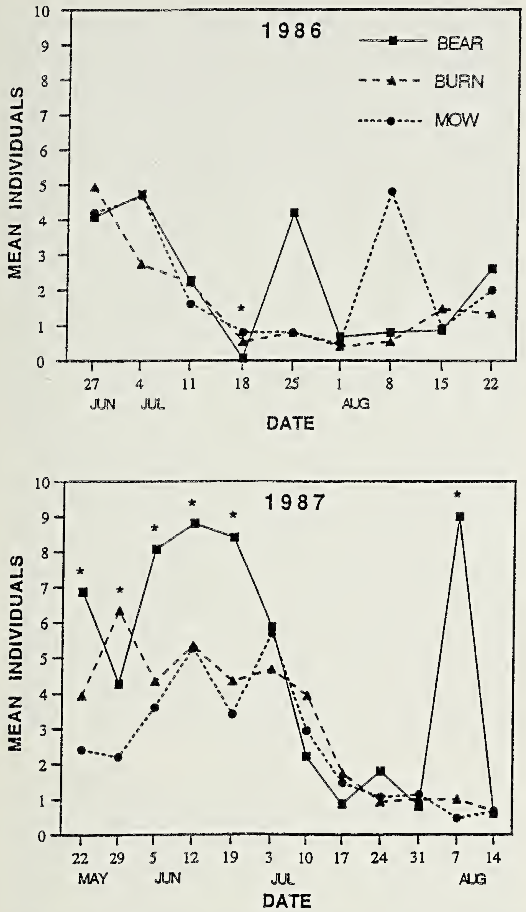

Figure 3.—Mean number of spider individuals, by treatment (mow, burn, bear), captured in pitfall traps, blueberry fields, Washington County, Maine; 1986, 1987, for each trapping date (n = 15 traps/treatment). ANOVA and DMRT; significance level: ★ = $P < 0.05$.

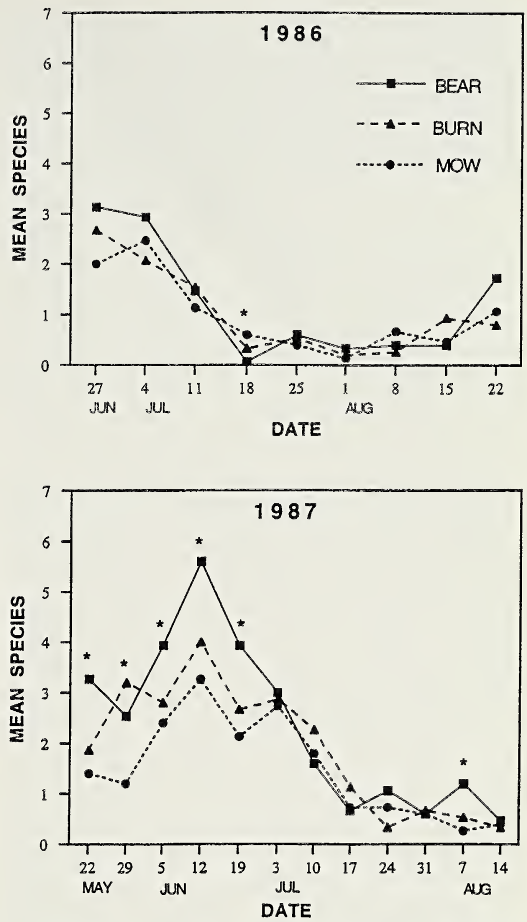

Figure 4.—Mean number of species, by treatment (mow, burn, bear), captured in pitfall traps, blueberry fields, Washington County, Maine; 1986, 1987, for each trapping date (n = 15 traps/treatment). ANOVA and DMRT; significance level: ★ = $P < 0.05$.

July; however, slight increases were noted in late August. Mean numbers of individuals and species generally declined in all fields after 3 July in 1987.

To assess the potential impact of insecticide applications on mean catches of spiders, we examined the variability in catches of both individuals and species before and after such applications in 1986 and 1987. For bear fields in 1986, there were no significant reductions in mean catches of either individuals (ANOVA, F = 0.60, df = 12) or species (ANOVA, F = 0.51, df = 12) of spiders immediately following application of phosmet to one bear field in early July. However, we detected some variability among replications for both mean catches of individuals (ANOVA, F = 8.23, df = 12) and species (ANOVA, F = 8.30, df = 12) following application of azinphos-methyl to one bear field in 1987. Nonetheless, this variability could not be attributed solely to application of the insecticide because differences occurred in both treated and untreated fields.

Faunal similarities.—Percentage similarity (*PS*) of species quantities among treatments was generally > 60%, but variable (Table 5). These similarity coefficients were greater in 1986 than in 1987. Comparisons that included the burn treatment had slightly greater *PS* values in 1986; however, this pattern was not evident in 1987 (Table 5).

Table 5.—A comparison of percentage similarity coefficients for spiders associated with three blueberry cultural treatments (Mow, Burn, Bear), Washington County, Maine, 1986, 1987. (*PS* = Bray-Curtis similarity index; BASIC program SUDIST.BAS (Ludwig & Reynolds 1988)).

	Treatment comparison		
Study year	Mow-Burn	Mow-Bear	Burn-Bear
1986 (9 weeks)	77.9	68.9	73.1
1987 (9 weeks)	62.8	64.8	56.8
1987 (12 weeks)	60.4	62.4	62.1

Community comparisons.—As expected, the terricolous spider fauna associated with blueberry fields we sampled in Maine had more species in common (i.e., higher *QS* values) with terrestrial habitats than with arboreal habitats (Table 6). For terrestrial habitats, many species of Lycosidae were shared in common between blueberry fields and spruce-fir forests of Maine (Jennings et al. 1988; Hilburn & Jennings 1988). These included species of *Pardosa*, such as *P. hyperborea* (Thorell), *P. moesta* Banks, and *P. xerampelina* (Keyserling), and species of *Pirata*, such as *P. insularis* Emerton and *P. minutus* Emerton. Arboreal-terrestrial species in common included *Grammonota angusta* Dondale, *Neoscona arabesca* (Walckenaer), *Philodromus placidus* Banks, and *Xysticus discursans* Keyserling.

Studies that employed the same sampling methodology as used in Maine's blueberry fields (i.e., pitfall traps) had higher *QS* values than those that employed radically different methods (e.g., pruned branches) (Table 6).

DISCUSSION

Spider taxa.—Our pitfall-trap catches indicate that the terricolous spider fauna associated with blueberry fields in Washington County, Maine is comprised chiefly of hunting spiders. Few species and few individuals of web-spinning spiders are captured in pitfall traps placed in these habitats. These results are consistent with similar pitfall-trap studies (Uetz 1975; Hilburn & Jennings 1988; Jennings et al. 1988) where the hunter guild is dominant among trap catches. No doubt other sampling methods (e.g., quadrat, D-vac, sweep net) would yield additional species and individuals of both web-spinner and hunter foraging guilds. Because most web-spinners are relatively sedentary compared to the more active, cursorial hunters (Gertsch 1979), pitfall traps capture few web-spinning species of spiders (Uetz 1975). Nevertheless, there are exceptions where species of web-spinning spiders (e.g., wandering species of Agelenidae, Hahniidae, and Linyphiidae) frequently occur in pitfall-trap catches (Jennings et al. 1988; Hilburn & Jennings 1988).

Because so few of Maine's diverse habitats have been investigated extensively for spiders, our collections from blueberry fields of Washington County provide new habitat association data and range extensions for many of the species. Of particular interest are collections of *Oreonetides* sp. 1, *Alopecosa kochi* (Keyserling), *Ebo iviei* Sauer & Platnick, and *Xysticus winnipegensis* Turnbull, Dondale & Redner. The linyphiid, *Oreonetides* sp. 1, apparently is undescribed and has been taken from dense, spruce-fir forests of Piscataquis County, Maine (Jennings et al. 1988). Our collections of *Alopecosa kochi*, *Ebo iviei*, and *Xysticus*

Table 6.—Comparison of spider faunas in different communities and habitats of Maine (*QS* = Sørensen's Similarity Quotient). Species identified only to generic level were excluded.

Community	Habitat	Sampling method	*QS*	Source
Spruce-fir	Ground	Pitfall traps	28.8	Hilburn & Jennings (1988)
Spruce-fir	Ground	Pitfall traps	28.4	Jennings et al. (1988)
Spruce-fir	Tree	Pruned branches	7.8	Jennings & Collins (1987)
Spruce-fir	Herb-shrub	Malaise traps	7.3	Jennings & Hilburn (1988)
Spruce-fir-mixed hardwoods	Ground	Litter expellant	7.2	Jennings et al. (1990)
Spruce-fir	Tree	Pruned branches	6.8	Jennings & Dimond (1988)
Spruce-fir	Tree	Pruned branches	3.8	Jennings et al. (1990)

winnipegensis extend the known ranges for these species in the United States. The lycosid, *A. kochi*, occurs principally in the western United States; however, it has been taken as far north as southern Ontario and Massachussets (Dondale & Redner 1979). The philodromid, *E. iviei*, is known from the western United States and western provinces of Canada, and prior to this study, as far east as Massachussets (Sauer & Platnick 1972; Dondale & Redner 1978). Before our study, the thomisid, *X. winnipegensis*, was known from very limited habitats and localities of Manitoba and New Brunswick, Canada (Dondale & Redner 1978).

Spider numbers, life stages, sex ratios.—We are unable to fully explain the apparent disparity in trap catches of spiders between study years. Why were there more spiders and more species of spiders captured in 1987 than in 1986? Possible causative factors include: differences in microhabitats studied each year and between years; temporal differences in sampling periods between years, and possible differences in potential-prey abundances between years.

Numerous features of the habitat can influence spider abundance (for a review, see Riechert & Gillespie 1986). However, other than the three blueberry cultural treatments (mow, burn, bear), we did not measure habitat parameters such as plant cover, litter depth, or moisture gradient. Because of scheduled treatments by blueberry growers, our study design required selection of new sites in 1987. Hence, sampling sites differed between years. The blueberry fields of Washington County, Maine represent a mosaic of diverse microhabitats, with varying soils, litter, and plant structure. Possibly some of the sites selected in 1987 were more favorable and, consequently, supported greater populations of spiders than sites selected and studied in 1986.

Although the same number of traps was used both study years (5 traps/field $\times$ 3 fields/treatment $\times$ 3 treatments = 45 traps/year), sampling duration varied between years (9 trap weeks, 1986; 12 trap weeks, 1987). Hence, the longer sampling period in 1987 may account for some of the observed differences in spider abundance between study years. When the first three weeks of trapping in 1987 were excluded, spider abundance remained greater in 1987 (Σ = 1260) than in 1986 (Σ = 832). Likewise, spider species composition remained greater in 1987 (Σ = 59) than in 1986 (Σ = 50). We suspect that factors other than sampling duration were responsible for between-year disparities of some individual species, e.g., *Pardosa xerampelina* (Keyserling) (Table 1).

Many spider families have stenochronous species that reproduce in spring and summer (Schaefer 1987); hence, we expected juveniles to be abundant among trap catches. However, juveniles comprised < 30% of total trap captures in the blueberry fields each year. Apparently our trapping periods (20 June–22 August 1986; 15 May–14 August 1987) spanned the time when many spider species reached sexual maturity, but before offspring were produced. Offspring (young spiderlings) were evident in some of our trap catches, especially in late July and early August 1986, and again in early August 1987. Some traps yielded 44–66 young lycosid spiderlings (probably *Schizocosa communis*) of similar size, shape, and coloration, which possibly indicates that these spiderlings came from the same clutch.

The preponderance of male spiders in our trap catches is not unusual because pitfall traps are selectively biased toward capture of wandering cursorial spiders (Uetz & Unzicker 1976). Male spiders generally are more mobile and may move considerable distances in search of mates; hence, the sexes are seldom equally represented in pitfall-trap catches (Hallander 1967; Muma 1975; Jennings et al. 1988; Hilburn & Jennings 1988).

Species richness, diversity, evenness.—Our results for these parameters are somewhat conflicting and inconsistent between study years. Intuitively, we predicted that the bear treatment would have the greatest and most diverse assemblage of spiders. The bear treatment was the least disturbed of the three treatments studied. However, our results indicate that species richness and diversity of spiders vary unpredictably and inconsistently among the three blueberry cultural treatments (Table 2). The only consistent trend observed was that spiders were more evenly distributed among species in the burn treatment, both study years. We suspect that factors other than cultural treatment *per se* were responsible for the observed variability in richness, diversity, and evenness of spiders. Uetz (1975) found that species diversity of spiders in an oak-tu-

liptree-maple forest of Delaware was significantly correlated with prey abundance; he also found that litter depth and habitat space were important determinants of within-habitat species diversity. Because predators often hide in dense litter, the effects of mowing and burning on litter structure and depth in Maine's blueberry fields warrant future investigation.

Treatment effects.—The pitfall-trap methods used during this study yielded inconsistent results regarding possible treatment effects on mean numbers of individuals and species of spiders trapped in blueberry fields. In general, more individuals and more species of spiders were trapped in the least disturbed habitat (i.e., bear fields); however, these were not consistent between study years (Table 4). Because of habitat perturbations and resultant changes in litter-plant structure, we had expected that fewer individuals and species of spiders would be caught in the burn and mow treatments. However, our pitfall-trap results yielded few significant differences among all treatments (Table 4). We suspect that timing of burn and mow treatments, depth or intensity of fire burn and the elapsed time between these perturbations and our study period may all have been significant factors influencing mean catches of spiders.

The burn treatments were accomplished in November (about seven months prior to commencement of pitfall trapping) each study year. Burning generally acts as a sanitation procedure by removal or reduction of plant structure and litter (Ismail & Yarborough 1981). Blueberry fields burned in the fall have several months to recover before the next growing season. This prolonged time period also may allow recolonization by spiders since aerial dispersal and colonization of neighboring habitats are common phenomena among spiders (Bishop 1990; Bishop & Riechert 1990; Greenstone 1982, 1990). The following spring after fall burning, the blueberry plants put on new growth. Such growth provides habitat space and attracts potential prey for spiders.

Conversely, spring burning may have detrimental effects on spider populations immediately after burning and during the growing season. Several investigators have reported declines in spider numbers following spring burning of grasslands and prairies (Rice 1932; Riechert & Reeder 1972; Nagel 1973; Dunwiddie 1991). The effects of spring burning on arthropod populations in blueberry fields are unknown.

The mow treatments for this study were accomplished in April, about 1–2 months prior to pitfall trapping. Although these treatments were less drastic perturbations (i.e., creation of litter and debris) than burning, far less time elapsed between mowing and pitfall trapping than between burning and trapping. In general, fewer spiders and fewer species of spiders were trapped in the mow treatment compared to the burn treatment; however, only one such comparison was statistically significant (i.e., species trapped, 12 weeks, 1987 (Table 4)). Because of the short time interval between mowing and trapping, spiders had less time to recover and colonize the mow fields. For European hay meadows, Nyffeler & Breene (1990) found that 40% fewer spiders were captured in pitfall traps after mowing. They also concluded that mowing frequency decreased spider populations sampled by sweep net. In Maine, flail mowing may result in increases in pest populations in lowbush blueberry fields (Forsythe & Collins 1988; DeGomez et al. 1990). Such pest populations are potential prey for spiders; however, there may be a lag time between predator-prey population buildup.

We suspect that some of the yearly differences in mean trap catches of spiders (Table 4) may be due to temporal changes in prey density and diversity. Warren et al. (1987) and others have suggested that changes in spider populations may reflect changes in prey density and prey diversity. Pest insect populations in Washington County, Maine in 1986 were generally low, and with few outbreaks reported (Forsythe & Collins 1986). However, in 1987 a variety of pest insects infested blueberry fields throughout Washington County (Forsythe & Collins 1987). Blueberry spanworm larvae, *Itame argillacearia* (Packard), were present in many fields and larval feeding damage was observed from early May through late June. High larval populations of blueberry flea beetle, *Altica sylvia* Malloch, also were noted in 1987. Blueberry sawfly, probably *Neopareophora litura* (Klug), began appearing in high numbers in June 1987 (Forsythe & Collins 1987). Because spiders respond to increases in prey density (Riechert & Gillespie 1986) and abundance of prey in-

fluences habitat (e.g., herbivory), differences in pest insect population levels may explain some of the observed differences in spider abundance between study years.

Faunal similarities.—The relatively high (> 60) percentage similarities of spider species quantities observed between treatment comparisons (mow–burn, mow–bear, burn–bear) are not unexpected because the treatment habitats were similar in plant-species composition and plant structure. Habitat structure and diversity are variables that affect spider species composition and abundance (Greenquist & Rovner 1976; Riechert & Gillespie 1986). Because the comparisons that included the burn treatment had slightly higher similarity coefficients, we conclude that the burn treatment had minimal effects on spider-species composition. This conclusion is supported by the generally greater species diversity indices (Table 2) observed for the burn treatment in 1987. Similar indices in 1986 indicated that the burn treatment ranked third in species richness, and second for species diversity (H').

Community comparisons.—Our results are consistent with earlier findings, i.e., the araneofauna associated with similar terrestrial habitats have species of spiders shared in common (Jennings & Hilburn 1988). Dissimilar habitats, in this case terrestrial *vs.* arboreal, have few species in common. We also conclude that Maine communities with similarly dominant spider families (e.g., abundant Lycosidae) are apt to share species in common. Geographical location and spider species distributions also are factors that may influence such community comparisons (Jennings & Collins 1987). Evidently, sampling methodology should not be ignored, because both habitat and sampling method may influence the determination of which species are shared in common.

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FORAGING ACTIVITY AND BURROW DISTRIBUTION IN THE SYDNEY BROWN TRAPDOOR SPIDER (*MISGOLAS RAPAX* KARSCH: IDIOPIDAE)

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ABSTRACT. Burrow-associated behavior of *Misgolas rapax* was observed in the field and laboratory. Spider density was estimated on 16 replicate plots at one study site in Brisbane Water National Park, NSW, Australia. These estimates were compared to habitat features including vegetation, topographic slope and soil penetrance. Spider burrow density varied significantly across the study plots and was significantly aggregated. There were no detectable patterns of relationship between habitat features and variation in *M. rapax* density. *Misgolas rapax* density and activity patterns were not related to natural variation in spatial and temporal patterns of prey-abundance. Field and laboratory experiments were conducted to determine the influence of proximate feeding history on activity in adult females. Foraging activity decreased after food supplementation in the field and was lower among the high-food treatment females in the laboratory. Despite the fact that *M. rapax* behavior is influenced by feeding history, these spiders are apparently unable to adjust their behavior to the unpredictable fluctuations in prey availability.

The Sydney brown trapdoor spider (*Misgolas rapax* Karsch 1878) is abundant in a variety of dry sclerophyll woodland habitats in SE coastal New South Wales, Australia. It builds a burrow lacking a trapdoor, but the entrance is occasionally sealed with silk and covered with leaves. Prey are captured from ambush at the burrow entrance, and adults rarely wander more than a few centimeters from the burrow. The sole exception to this pattern is the mate-searching behavior of males. One striking aspect of the biology of *M. rapax* is that an occupied burrow is either open or closed (sealed with silk) for long periods of time (weeks to months). Individuals of *Misgolas rapax* can be found at the entrance to their burrows waiting for prey in any month of the year. This pattern contrasts with other trapdoor spiders which aestivate for long periods during the summer months (Buchli 1969; Marples & Marples 1972) or dry periods (Main 1982). The current study was initiated to determine if proximate environmental factors, or the abundance of prey, might influence the foraging activity patterns of this species. Another pattern in this species is the tendency for many burrows to be located in some areas and few in adjacent, apparently similar, areas. This work on *M. rapax* was conducted at the same time on the same study plots as similar work on the common orb-weaving spider *Argiope keyserlingi* Karsch 1878. In that species, density was related to features of vegetation that provided favored web sites (Bradley 1993). A second goal of the study was to examine the burrow density and dispersion patterns of *M. rapax* and their relationship to features of the habitat.

METHODS

Study site.—The study area was located in Brisbane Water National Park (33°33′S, 151°18′E) at the SE corner of the town of Pearl Beach, New South Wales, Australia. A set of sixteen 0.023 ha plots (15m × 15 m) was marked with wood corner posts. The plots were established on one hillside in a patch of dry sclerophyll woodland dominated by *Casuarina torulosa* (70% by frequency) such that no two plots were closer to each other than 5 m. Consult Bradley (1993) for a detailed description of the study plots and general study site. Other large burrowing spiders known from the study area included *Atrax robustus* Cambridge 1877, *Geolycosa godeffroyi* (L. Koch) 1865, *Hadronyche* sp.?, *Lycosa furcillata* L. Koch 1867, *Lycosa pictiventris* L.

Koch 1877 and *Misgolas gracilis* (Rainbow & Pulleine 1918).

Environmental measurement.—Weather records (rainfall, temperature) were obtained from the Crommelin Biological Research Station, a station within 500 m of the study area. Soil temperature (surface, 15 cm and 30 cm), air temperature, and relative humidity were continuously recorded with a Weathertronics thermograph and hygrothermograph located in a ventilated wooden box on the study area. Temperature and humidity were measured at the burrow entrance for each spider activity observation using a Novasina MIK-2000 portable hygrothermograph (Novasina AG, Zurich). Soil penetrance was measured with a Soiltest CL-700 penetrometer; 100 measurements were made on each plot using a stratified random sampling design. This device provides an indication of surface resistance, which has been implicated as an important factor in the choice of burrowing site in studies of other arachnids (Lamoral 1978; Bradley 1986; Polis & McCormick 1986). Average topographic slope was estimated for each plot by estimating total elevation change from highest to lowest point on the plot. Twelve vegetation variables (Bradley 1993) were subjected to principal components analysis. The principal component scores for each plot along the first two axes were compared to measures of *M. rapax* density using Pearson product-moment correlation. The dispersion pattern of burrows was analyzed using the variance/mean ratio method (Southwood 1966). Significance of this ratio was assessed by Kershaw's method of calculating t (Kershaw 1973).

Burrow characteristics.—Burrows of 48 adult *M. rapax* were excavated (a large hole was dug beside the burrow, which was then approached from the side); spiders were collected from 34 of these burrows and the midden of rejected prey remains (rejectamenta) was collected from 32 burrows. All rejectamenta were identified and a minimum number of prey of each taxon was estimated from the parts. Burrow depth, diameter at entrance (just below flared opening at point where burrow becomes cylindrical), orientation of opening, depth of protective silk-closure, and depth of midden were measured. Spider fang length (right), carapace length and the length of tibia I (right) were measured to 0.1 mm.

Spider activity measurement.—Burrow entrances were marked with numbered wood tongue depressors placed 30 cm S of the entrance (n = 429). Regular (approximately biweekly, on the same nights as prey samples) observations of marked burrows were made to determine if they were open and whether the spider was near the entrance. At each visit to a marked burrow, the temperature and relative humidity were also measured. Spider population density was estimated during December 1985 by counting the number of occupied burrows on each plot.

Prey abundance measurement.—Two measures of prey abundance were made. Samples of leaf-litter were collected adjacent to the study plots by removing all litter down to bare soil from a 0.25 m^2 area. Potential prey organisms were extracted using a modified Tullgren funnel (Southwood 1966). Two rows of five pitfall traps were placed on each plot; pits were separated by 2 m, and rows were 3 m from edge of plot. Pits 20 cm deep were constructed of 5 mm thick polyvinyl chloride tubing with an inside diameter of 11 cm buried flush with the soil surface. A removable sleeve was used within pits fitted on the bottom with 0.5 mm nylon mesh for drainage. Pits were covered when not in use but were left dry and open during sampling. Samples were collected over 24-hour periods on 18 dates between August 1994–February 1996. Potential prey captured from litter or pitfall samples were identified (usually to family) and measured to nearest 1 mm (body length). Dry-weight biomass was estimated using regression equations appropriate for each taxon (Rogers et al. 1976, 1977). In cases where no appropriate regression equation was available, one was calculated from specimens captured in the study area. Potential-prey samples (litters, pits) were compared to temporal patterns of *M. rapax* activity using Pearson product-moment correlation analysis of prey variables against the proportion of *M. rapax* burrows that were open with an active spider near the entrance. Prey samples were also compared to *M. rapax* density spatially (across plots) using ANOVA (repeated-measures design).

Laboratory feeding experiment.—Twenty-four adult female *M. rapax* were installed in individual 30 cm (tall) × 30 cm (deep) × 7 cm (wide) clear acrylic plastic ("Plexiglas") containers. Each container was first filled to

within 5 cm of the top with natural soil from near the study area. The spiders readily dug burrows in the containers and lined them with silk. The soil was kept damp with regular misting of distilled water. All spiders were housed in a room illuminated on a 12:12 cycle and maintained between 21–29 °C. Spiders were randomly divided into two groups. One group (high-food) was fed either one adult cricket (*Gryllus* sp.), one ultimate-instar mealworm larva (*Tenebrio molitor* Linnaeus) or one adult mealworm beetle every other day. All prey items were weighed to the nearest 0.1 mg. The second group (low-food) was fed a similar meal once per 14 days. Spiders were only fed if they were in the "foraging position" within 3 cm of the top of the burrow entrance. The food item was presented to the spider by gently rubbing the silk near the entrance to the burrow until the spider grasped the item. If a prey item was not eaten, it was removed the following day. Each spider was weighed at the beginning (27 October 1984) and end of the experimental period (2 September 1985). For the test of differences in activity (proportion of nights in foraging position), the proportions were subjected to the arcsin transformation before analysis.

Field food-supplementation experiment.—Seventy-three active (in foraging position) adult female *M. rapax* were located and their burrows marked. Spiders were randomly divided into two groups. Spiders in one group (food-supplementation, n = 30) were fed one seventh (ultimate) instar mealworm larva on four successive nights (13–16 February 1986). The mealworm was presented to the spider by gently rubbing the silk near the entrance to the burrow until the spider grasped the mealworm. Spiders in the second group (unmanipulated, n = 43) were checked for activity by rubbing the silk, but they were not fed. No attempt was made to restrict natural capture of prey. All spiders were checked subsequently on 20 February and 10 March 1986; the spider was scored for activity and for whether the burrow entrance was open or closed (with silk).

RESULTS

Burrow characteristics.—Burrows of *M. rapax* were found in the loosely consolidated sandy soils across the entire study area. Burrows were lined with silk that was attached to the *Casuarina*-needle litter at the entrance. There were few attached radially-arranged leaf or twig lines, which are common features of other trapdoor spider (*Aganippe* O. Pickard-Cambridge 1877 and *Idiosoma* Ausserer 1871) burrows found in areas with a substantial leaf litter (Main 1984). Burrows were relatively vertical silk-lined tubes with a mean depth of 33.6 cm (SD = 8.1, n = 47) and mean entrance diameter of 22.3 mm (SD = 2.6, n = 48). Only 10% of the burrows contained a defensive-sock closure (mean depth of closure 16.0 cm; SD = 3.1; n = 5). Main (1984) also mentions the inconsistency of defensive-sock closures in *M. rapax* burrows. Most of the spiders located in excavated burrows were found at the bottom; some were found just below the silk closure, holding it closed with their chelicerae. The mean burrow depth was correlated with mean entrance diameter (r = +0.26, P < 0.05). Burrow diameter was correlated with spider carapace length (r = +0.50, P < 0.01) and fang length (r = +0.49, P < 0.01). The burrow opening of most *M. rapax* burrows was tilted at an angle. There was no significant bias to the orientation of the openings with respect to either slope or compass direction. Many burrows contained a midden of uneaten prey remains near the bottom of the burrow (mean depth 19.8 mm; SD = 10.5; n = 26).

Density and habitat relationships.—*Misgolas rapax* density varied by a factor of 6.4 across the study plots. The mean density estimate based on occupied burrows in December 1995 for all 16 plots combined was 391/ha (n = 16, SD = 236). Vegetation, elevation, and slope characteristics varied significantly across the plots (Bradley 1993) but there were no correlations with *M. rapax* density patterns. There was significant variation in soil penetrance across plots (ANOVA; F = 12.9; df = 15, 1584; $P \ll 0.001$), but this feature was not correlated with *M. rapax* density (r = − 0.35, ns). The mean distance between burrows was 5.4 m (SD = 9.0). The dispersion of *M. rapax* burrows was significantly clumped with a variance/mean ratio of random point-to-burrow distances of 14.8 (t = 13.9, P < 0.01). This may reflect the tendency for young spiders to disperse relatively short distances from the maternal burrow before constructing their own burrows.

Activity patterns in field.—to assess "ac-

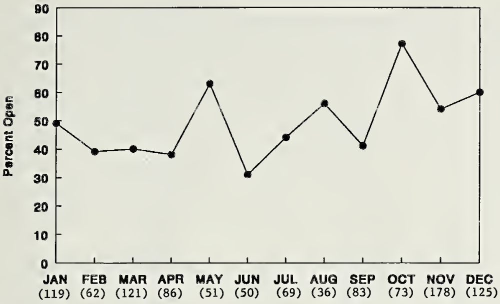

Figure 1.–Annual activity patterns of *Misgolas rapax*. The values in the figure represent the percentage of marked burrows which were open (active) and known to contain a live spider. The sample size of burrows checked is included in parentheses below the month.

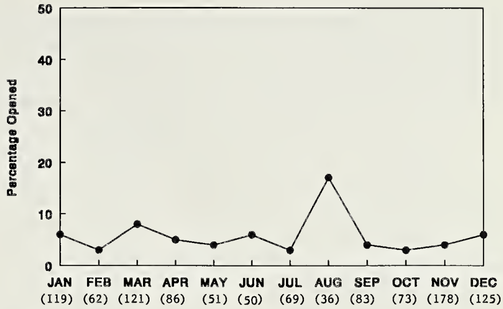

Figure 2.–The proportion of *Misgolas rapax* burrows that were discovered newly opened during the month indicated. The sample size of burrows checked is included in parentheses below the month.

tive" spiders, I analyzed observations of marked burrows. If a marked burrow was discovered closed and was never observed open again during the study, it was assumed that the spider had died or abandoned the burrow, and it was removed from the sample. Of the 429 marked burrows, activity data were scored for 1053 observations from 253 burrows known to contain a living *M. rapax* individual. These observations were made between September 1984–February 1986. The pattern of annual activity as indicated by the proportion of open burrows that were known to contain a living *M. rapax* is not strongly seasonal (Fig. 1). Similarly there is no obvious seasonal pattern to the proportion of previously-closed burrows which were opened during a particular month (Fig. 2). Burrows tended to remain open for long periods ($\bar{x}$ = 83 days, SD = 65, range 1–397 days). After a spider sealed the entrance to its burrow with silk, it typically remained closed for an extended interval ($\bar{x}$ = 76, SD = 60, range 6–332 days). On any given visit a burrow had a probability of 49.6% of being found open. Active *M. rapax* are usually visible near the entrance to the burrow (within three cm of the opening). The number of spiders in this foraging position was assessed during 722 observations at open burrows. Significantly more spiders were observed in the entrance of open burrows at night (18%) than during the day (7%) ($t = 2.3$; $P < 0.05$). There were no significant correlations between surface temperature, soil temperature or surface humidity and the tendency for a burrow to be open, or for the spider to be in the active foraging position.

Relationship to potential-prey phenology.—Prey remains analyzed from the middens in excavated *M. rapax* burrows reveal that this spider eats substantial numbers of the large and aggressive bulldog ant *Myrmecia gulosa*. Unfortunately, the remains in middens undoubtedly contain a biased sample of prey; large and hard-bodied prey are probably over-represented (Table 1).

A total of 2715 potential prey items was captured in the pitfall samples (this total excludes species known to be rejected by *M. rapax* in the laboratory). Prey availability (num-

Table 1.—Identified prey remains found in *Misgolas rapax* burrows (n = 287 prey; n = 32 middens).

Prey category	Percentage of burrows	Percentage of all prey
Myrmecia (Formicidae)	78	46
Carabidae	50	18
Scarabaeidae	41	5
Formicidae (others)	34	5
Coleoptera	28	4
Curculionidae	19	2
Hemiptera	13	2
Blattodea	13	1
Camponotus (Formicidae)	9	2
Cerambycidae	9	<1
Hymenoptera (others)	9	<1
Scorpionida	3	1
others	n/a	12

Table 2.—Results of the laboratory feeding experiment. [1]The sample size reflects differences in number of spiders surviving at the time of measurement. [2]The proportion of nights when a spider was seen in the "feeding position" within 3 cm of the top of the burrow.

Variable	High-food			Low-food			Significance	
	$\bar{x}$	SD	n^1	$\bar{x}$	SD	n^1	t	P
Number of meals	14	(9.1)	11	8	(2.9)	12	2.09	ns
Initial spider mass	2.38	(0.77)	12	2.47	(0.74)	12	−0.29	ns
Total food mass (g)	2.60	(1.44)	11	1.22	(0.43)	12	3.05	<0.05
Final spider mass (g)	2.83	(0.72)	11	2.36	(0.38)	12	−2.02	<0.05
Change in mass (g)	0.56	(0.73)	11	−0.11	(0.56)	12	−2.51	<0.05
Prop. nights active[2]	0.15	(0.13)	11	0.27	(0.16)	12	−2.13	<0.05

bers trapped) appears to vary significantly through the season as assessed by pitfall-trap samples (ANOVA $F = 2.17$; $df = 15, 272$; $P < 0.01$). Numbers and biomass of potential-prey both peak during spring or early summer (late September through December). Results from the litter samples appear less seasonal (ANOVA ns). Using proportion of spiders active (open burrow with spider near entrance) as an index of *M. rapax* temporal foraging phenology, there was a weak correlation with total potential-prey numbers captured in the pitfall-trap samples ($r = +0.57$; $P < 0.05$); this correlation disappears when the sample is restricted to the larger potential prey that comprise most of the diet of *M. rapax* ($r = +0.38$; ns). Similarly, there is no seasonal correlation with potential-prey biomass ($r = +0.42$; ns). There were no signficant correlations between *M. rapax* foraging phenology and potential prey in the litter samples.

Spatially, potential-prey abundance varied signficantly across the study plots for numbers ($F = 2.17$; $df = 15, 272$; $P < 0.01$) but not biomass (ANOVA $F = 0.71$; $df = 15, 272$; ns). There was no spatial correlation between potential-prey patterns of numbers or biomass and *M. rapax* density ($r = +0.0008$ ns; $r = 0.36$ ns).

Laboratory experiment results.—The feeding behavior of *M. rapax* confounded the treatment effect in this experiment. After eating the first few (2–4) successive meals, many of the high-food treatment spiders ceased feeding. They often remained at the bottom of their burrow and would not respond for days or weeks. Even though they were offered food, they did not feed. This diluted the differences in food consumed between the two treatments (Table 2). Nevertheless, the total food consumed by the spiders in the two treatments differed. The high-food treatment spiders ate significantly more and were significantly heavier at the end of the experiment (Table 2). High-food treatment females gained 24% and low-food treatment females lost 4% of initial body weight. High-food treatment females were also significantly less active (less often in foraging position) than low-food females (Table 2). Spider growth was positively correlated with the number of meals eaten ($r = +0.87$; $P < 0.01$). When this relationship is plotted, the "break-even point" or the number of meals eaten over the 11 months that resulted in no weight change was approximately four meals (Fig. 3).

Field experiment results.—Of the 43 spiders in the unmanipulated group, most kept their burrow open through 20 February, but 38% had closed their burrow by 10 March (Fig. 4A). On 10 March, 59% were still active at the top of their burrow. Among the 30 spiders in the food-supplementation group, only 45% had open burrows by 10 March (Fig. 4B). Fewer of the food-supplementation group remained active; by 20 February this proportion of active individuals was significantly lower than among the unmanipulated group (Fig. 4). On 10 March, only 7% of the food-supplementation females were actively foraging, while 60% of the unmanipulated females were active (Fig. 4).

DISCUSSION

Density and dispersion.—One clear result of this study is that the burrows of *M. rapax* are clumped. Clumped dispersion patterns have been observed in a variety other mygalomorph species (Main 1982, 1987; Marples & Marples 1972; Coyle & Icenogle 1994) and

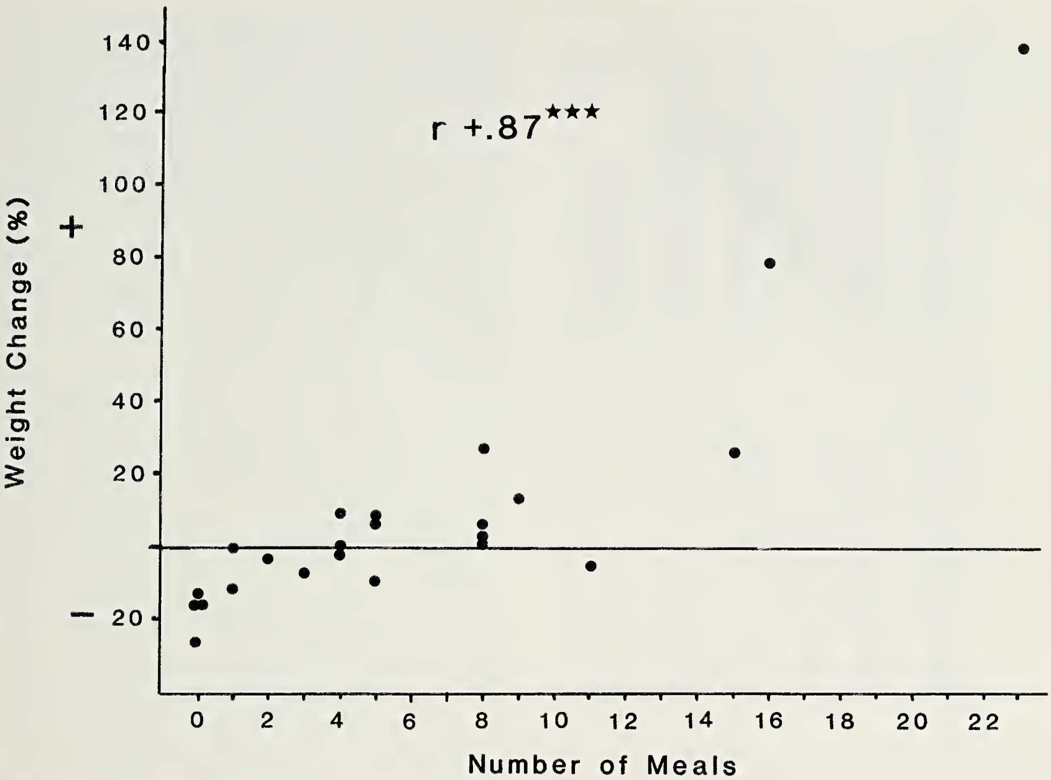

Figure 3.–The weight gained (+) or lost (−) during the laboratory feeding experiment as a percentage of initial spider weight compared to the number of meals eaten by an individual female *M. rapax*. The horizontal line represents no change in weight. These two variables are positively correlated ($r = +0.87$, $P < 0.001$).

burrowing Lycosidae (Humphreys 1976; Fernández-Montraveta et al. 1991). It is possible that the aggregation of *M. rapax* burrows reflects limited dispersal from the maternal burrow, but I observed no tendency for peripheral burrows to be smaller nor a central large burrow indicative of a "matriarch" as described by Main (1978, 1987). It is possible that longevity and relatively low recruitment rates might obscure any such pattern.

The density estimates for *M. rapax* obtained in the current study (391/ha or 0.04/m²) are considerably lower than those published for other large burrowing spiders. Humphreys (1976) indicates that density in *Geolycosa godeffroyi* (L. Koch) was quite variable and locally high in relativley small areas of disturbed or edge habitat. Densities at Humphreys' Kowan study site range between 0.16–1.3 spiders/m² (Humphreys 1976; estimated from his fig. 5). Mature female density was about 0.01/m². *Geolycosa godeffroyi* is a large spider (mature female mass approximately 1.5 g, Humphreys 1976), but this is equivalent to only 63% of the size of a mature female *M. rapax* (2.4 g, this study Table 2). McQueen (1983b) studied *Geolycosa domifex* (Hancock) and observed extremely variable and high densities (5–13 spiders/m²). The spiders were not uniformly dispersed and average density over the entire field site rarely exceeded 1/m² (McQueen 1983b). Like *Geolycosa godeffroyi*, *G. domifex* is relatively smaller than *M. rapax* (mature female mass *ca.* 0.5 g; McQueen 1983a). One might expect that a large, long-lived mygalomorph such as *M. rapax* would be found at lower densities than the smaller lycosids. Other studies of mygalomorphs, however, have documented high population densities (Marples & Marples 1972; Fairweather 1993; Wishart 1993). Marples & Marples (1972) provide estimates ranging from 1.5–292 spiders/m² for *Cantuaria toddi* Forster in New Zealand. This re-

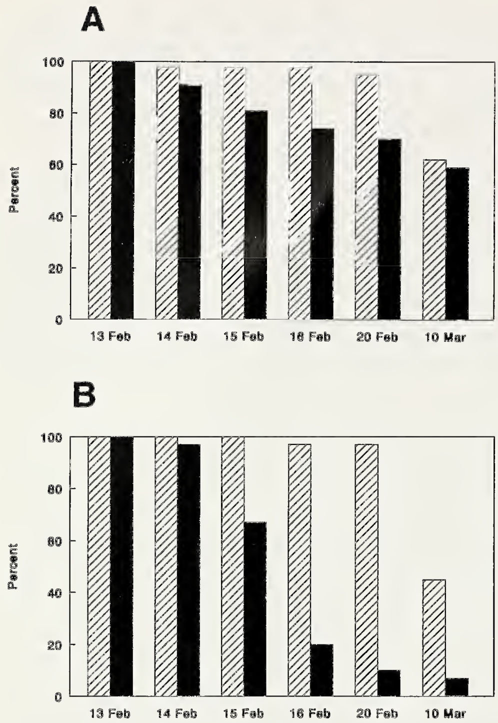

Figure 4.–The results of the field food-supplementation experiment. The percentage with open burrows (hatched bars) and the percentage where the spider was observed within three cm of the burrow entrance in the foraging position (solid bars) on the four feeding dates (13–16 February 1986) and subsequently on 20 February 1986 and 10 March 1986. (A) The percentage of open burrows and active spiders among unmanipulated (control) spiders, $n = 43$. (B) The percentage of open burrows and active spiders among food-supplemented spiders, $n = 30$.

markable range of densities reflects the fact that the burrows of *C. toddi* were found in dense clusters in restricted habitats such as cliffsides and road margins (Marples & Marples 1972). Fairweather obtained estimates of approximately 0.8–6.4 spiders/m^2 for *M. rapax* and 4–12 spiders/m^2 for *Misgolas gracilis* (Fairweather 1993; estimated from his fig. 1). Like Humphreys, Fairweather sampled in habitat patches that were in some cases near ecotones or edges. To some extent the "edge effect" (Leopold 1947) may have influenced the high population density estimates. A similar effect, attributed to remnant habitats and low predator density is cited by Wishart to explain the relatively high population densities of a series of mygalomorph species (Wishart 1993). Oxford (1993) conducted a long term (19 yr) study of local populations of the theridiid *Enoplognatha ovata* (Clerck) and found a consistent pattern of spiders found only near "verges of roads and tracks" mostly near dry-stone walls. A recent review indicates that ecotones support increased biodiversity and productivity (Risser 1995). It is not clear whether this edge effect might also be applied to the current study site which is near two small dirt roads and within ½ km of a major habitat discontinuity.

There was signficant variation in *Misgolas* density across the study area. I detected no signficant correlations between *M. rapax* density and any environmental variables (vegetation variables, slope, soil penetrance) or prey relative-abundance measures. Site-specific variation in density was also demonstrated for *M. rapax* by Fairweather (1993; his table 2). It is relevant to consider the spatial scale of the current study; all 16 study plots were within a patch of habitat 1.5 ha in extent. At this relatively small spatial scale, the observed density variation may reflect stochastic effects magnified by the aggregated dispersion pattern. At larger spatial scales, it is clear that *M. rapax* and other related mygalomorphs exhibit habitat specificity (Fairweather 1993).

One feature of this habitat that has the potential to create patchy distributions is fire. The frequency of fire in this area is relatively high. Main (1981) indicates that adults of fossorial species such as *Anidiops villosus* (Rainbow) survive fire in their burrows. Main (1995) pointed out that the post-fire environment, with reduced shade and litter, was often hostile. Main (1995) suggests that increased adult mortality and declining juvenile recruitment may result in long-term population declines in *A. villosus* after fire. Observations of *M. rapax* after a fire burned this area (in 1987 after the conclusion of this study) indicate that few, if any, individuals were injured. The fossorial habit of this species provided ample protection from fire in the short term. At Brisbane Water National Park plant communities and insects rebounded rapidly after bushfire so the likelihood that variation in prey distribution reflects fire-history is probably low. Fire was shown to have little effect on spider densities or communities in Québec (Koponen 1993) and in Germany (Schaefer 1980).

Activity patterns.—There appears to be

little demonstrable relationship between activity levels of *M. rapax* and proximate weather conditions or seasonality. Activity, as assessed by the proportion of burrows open or spiders near their burrow entrances, was low and unpredictable. This result contrasts with other work on sit-and-wait spiders whose activity levels are influenced by temperature (Buchli 1969; Ford 1978), rainfall, humidity or season (Buchli 1969; Shook 1978; Main 1981). *Misgolas rapax* do appear to forage primarily at night; in this respect it is similar to other trapdoor spiders (Buchli 1969; Coyle 1981) and the theraphosid *Aphonopelma seemanni* (F. P. Cambridge) (Herrero & Valerio 1986). In two species of large burrowing lycosid spiders, no diel periodicity was detected (Humphreys 1973; McQueen & Culik 1981). Other lycosids are strictly nocturnal, e.g., *Lycosa carolinensis* Walckenaer (Shook 1978).

One factor that has been shown to influence burrow closure in trapdoor spiders is rainfall (McKeown 1936; Main 1993). Foraging activity of *M. rapax* during rainstorms was very low, but insufficient data were collected during storms to evaluate this observation statistically. There is no indication in the data that more *M. rapax* burrows were found closed immediately after rainstorms. The soils in this study area are sandy and well drained. Even though the soil is occasionally saturated after heavy rain, there is little chance that standing water would persist. Main has suggested that one of the primary functions of the closable sock in the open burrows of *Misgolas* is to prevent flooding of the burrow (Main 1993).

There is no evidence that daily activity levels, seasonal activity patterns or population densities of *M. rapax* are responsive to variation in prey availability. On the other hand, results from the laboratory and field food-supplementation experiments indicate that well-fed individuals are significantly less active. One explanation for the lack of correspondence between spider activity and prey phenology is that prey availabiliy was not accurately measured by pitfall traps. Evidence against this interpretation is that the pitfall traps captured all of the known prey species, and that when pit data were altered to include only known prey species, there was even less relationship to spider activity patterns. It should be noted that I have little information about the proportions of prey in the natural diet of *M. rapax*. Thus, it is still possible that a subtle positive relationship between prey availability and spider activity exists which could not be detected by the methods I employed in this study.

A second plausible explanation for the results I obtained is that prey are too unpredictable in time and space to be tracked by variation in spider activity. Sedentary burrowing trapdoor spiders only detect prey a limited distance from their burrows (Main 1957; Buchli 1969). Perhaps the encounter rates with prey are too infrequent, and the variation in prey availability is too irregular for *M. rapax* to have evolved a mechanism that could predict prey encounters. In his review of foraging strategies of spiders, Uetz (1992) explains that in cases where differences in the fitness gain between behavioral strategies are small, one might not expect the evolution of a single optimum strategy.

Another explanation for the lack of a correspondence between activity patterns of *M. rapax* and potential prey is that the annual food requirements are so low that this effect is undetectable. As few as four meals/yr are sufficient for maintenance of body weight, and individuals consuming 20 meals/yr can double their body weight (Fig. 3). Many individuals provided with a few supplemental prey in the field experiment closed their burrows and/or became inactive. *Misgolas rapax* were shown to have extraordinarily long periods of inactivity in the field ($\bar{x}$ = 76 days) and may live many years as has been shown for other members of the family (Main 1981, 1982). Variation in prey availability as measured by the pitfall samples was evident from month-to-month, but with only a weak seasonal pattern. It seems that the temporal scale of variation in prey is too short relative to the patterns of activity/aestivation in *M. rapax*.

One last factor that may exert a powerful influence on activity of *Misgolas* is the risk of predation. It is possible that the long periods of burrow closure are a response to the risk of predation. Both of the chief predators of this species (wasps and legless lizards) enter burrows to attack *M. rapax*. Predatory wasps (Sphecidae, Pompilidae) which prey on spiders commonly inhabit the area of the current study. A large pompilid *Cryptochelius* (sp.?) was commonly observed hunting near the ground in the study area and is a potential

predator of *Misgolas*. One of the chief predators of *M. rapax* is the legless lizard *Pygopus lepidopodus* (Lacépède) (Patchell & Shine 1986). This species has been commonly observed on the study site, is broadly sympatric with *M. rapax* (Cogger 1983), and may be specialized for hunting large burrowing spiders (Shine 1986). Both *Pygopus lepidopodus* and the predatory wasps are diurnal or crepuscular. It is by no means certain that these predators influence the activity patterns of *M. rapax*, but this subject deserves further study.

I studied *M. rapax* at the same time and at the same locality as I conducted work on the orb-weaver *Argiope keyserlingi*. While *A. keyserlingi* density was directly related to measurable features of the vegetation (Bradley 1993), density of *M. rapax* was not. The simplest explanation for this difference is that *Argiope* actually use the vegetation as a framework to construct their snares. Local aggregations of *Misgolas* appear to reflect limited dispersal of juveniles and long persistance of individuals. Neither species appears to exhibit activity or density patterns that reflect prey availability. For both species the availability of prey appears to be unpredictable in both space and time. At larger spatial scales, there is no doubt that these spiders have habitat preferences (Fairweather 1993; Levi 1983).

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THREE NEW SPECIES OF *SELENOPS* LATREILLE (ARANEAE, SELENOPIDAE) FROM NORTHERN BRAZIL

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ABSTRACT. Three new species of *Selenops* (Araneae, Selenopidae) are described and illustrated, *S. ducke* and *S. kikay* (from both sexes) and *S. para* (from the female only), from northern Brazil.

RESUMEN. Se describe e ilustra tres nuevas especies de *Selenops* (Araneae, Selenopidae), *S. ducke* y *S. kikay* (conocidas por ambos sexos) y *S. para* (sólo por la hembra), para el norte de Brasil.

The fauna of Brazilian selenopids has been very well studied, and numerous species of *Selenops* Latreille 1819 have been reported for that country (Mello-Leitão 1918; Lins Duarte 1978). From additional collecting carried out there (e. g., in whitewater inundation forest near Manaus) and after revising a great number of American selenopids, I found some species new to science. Three of them, from northern Brazil, are described here.

METHODS

The material examined is deposited in the following collections: MCN, Museu de Cienciâs Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil and MNRJ, Museu Nacional Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Palpi and epigyna were dissected and cleared in lactic acid (90%), for 15–20 minutes in a double boiler. The format of abbreviations used follows Platnick & Shadab (1975). The terminology used for the male palp parts follows Coddington (1990), and the structures of the female genitalia were named as in Sierwald (1989). Measurements are in millimeters.

Selenops ducke new species
Figs. 1–5

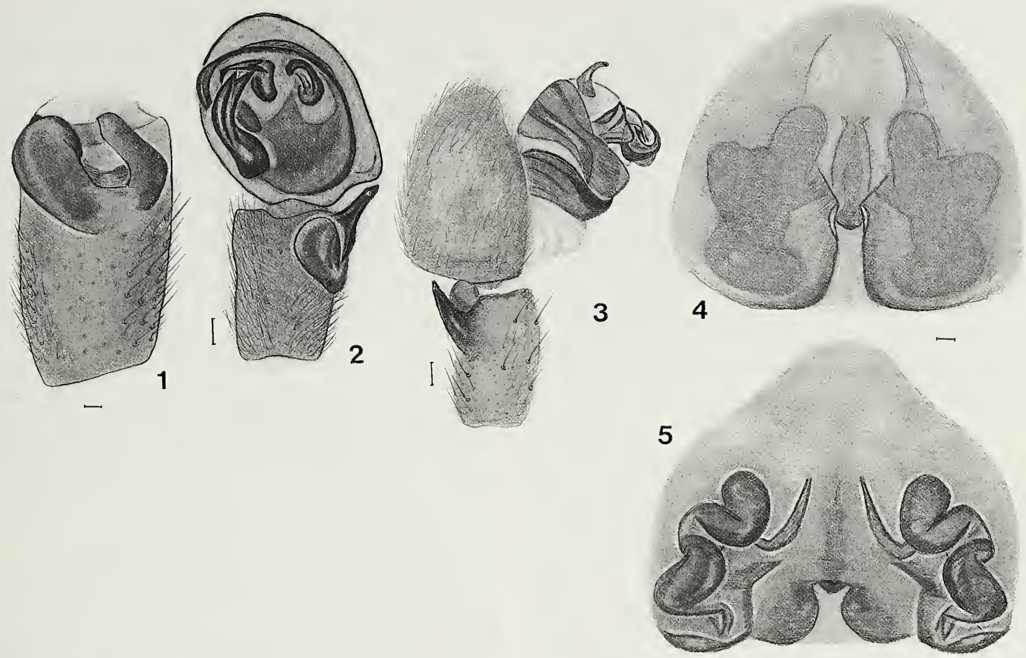
Types.—Male holotype and female paratype from Reserva Ducke, Manaus, Amazonas, Brazil. (17–24/VIII/1991, A. Brescovit), deposited in MCN (N° 25527 and 21487).

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—Males can be distinguished from those of ***S. kikay*** new species and *S. tomsici* Corronca (in press) by the form of the retrolateral tibial apophysis (Figs. 1, 2), fin-like conductor (Fig. 2) and short and flattened embolus (Fig. 3), females by an elongated middle field of the epigynum with a dark middle triangular area, and spermathecae with three curves (Figs. 4, 5).

Male.—Total length 6.50. Carapace 3.05 long, 3.10 wide. *Eye sizes and interdistances:* AME 0.23, ALE 0.15, PME 0.23, PLE 0.30, AME-AME 0.18, AME-ALE 0.40, AME-PME 0.08, PME-PME 0.78, PME-PLE 0.30, PME-ALE 0.28, PLE-PLE 1.50, ALE-ALE 1.33. Abdomen 3.45 long, 2.25 wide. Leg formula 2143. *Leg lengths:* I– femora 4.00, patellae + tibiae 5.50, metatarsi 3.40, tarsi 1.20, total 14.10, II– 4.70, 5.70, 3.80, 1.40, total 15.60; III– 4.40, 4.50, 2.90, 1.20, total 13.00; IV– 4.30, 4.40, 3.30, 1.30, total 13.30. *Leg spination:* femora I–IV p1–1–1, d1–1–1, r1–1–1; tibiae I–II p1–1–0, d0–1–0, r1–1–0, v2–2–2, III–IV p1–1–0, r1–1-0, v2–2–0; metatarsi I–II p1–1–0, r1–1–0, v2–2–0, III–IV p1–1–0, d1–1–0, r1–1–0, v1–1–0. Carapace pale brown. Chelicerae and legs gray-brown. Femora I-II with gray prolateral band, tibiae I-IV with two gray incomplete rings, metatarsi orange-brown. Abdomen pale gray-brown with dark transverse band at distal part and three or four lateral dark lines. Palp of male as in Figs. 1–3.

Female.—Total length 9.00. Carapace 3.50 long, 3.75 wide. *Eye sizes and interdistances:* AME 0.23, ALE 0.13, PME 0.28, PLE 0.33, AME-AME 0.23, AME-ALE 0.53, AME-PME 0.10, PME-PME 0.85, PME-PLE 0.48, PME-ALE 0.33, PLE-PLE 1.98, ALE-ALE 1.63. Abdomen 5.50 long, 3.50 wide. Leg formula 2143. *Leg lengths:* I– femora 4.50, patellae + tibiae



Figures 1–5.—***Selenops ducke*** new species. 1, Left palp, detail of tibial apophysis; 2, Left palp, prolateral view; 3, Left palp, ventral view; 4, Epigynum, ventral view; 5, Vulva. Scale = 0.20 mm.

5.40, metatarsi 2.90, tarsi 1.10, total 13.90, II–4.60, 5.50, 2.90, 1.10, total 14.10; III–4.70, 5.10, 2.80, 1.10, total 13.70; IV–4.30, 5.20, 3.20, 1.10, total 13.80. *Leg spination:* femora I p1–1–0, d1–1–1; II–IV d1–1–1; tibiae I–II v2–2–2, III–IV v1–0–0; metatarsi I–II v2–2–0, III–IV 1–1–0. Coloration as in male except metatarsi I–IV with two dark rings. Epigynum and spermathecae as in Figs. 4, 5.

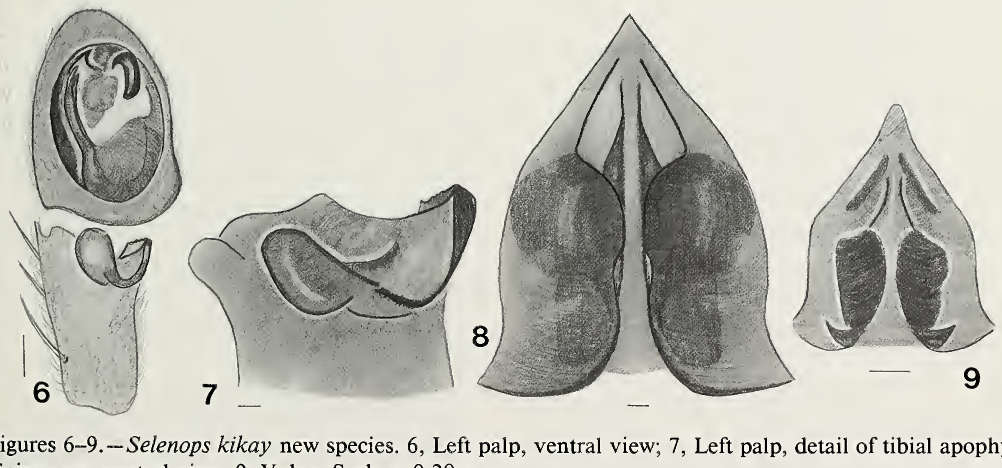
Material examined.—Only the types.

Distribution.—Known only from the type locality.

Selenops kikay new species
Figs. 6–9

Types.—Male holotype and female paratype from Itabuna, Bahía, Brazil, deposited in MNRJ (no collector or date).

Etymology.—The specific name is an arbitrary combination of letters.



Figures 6–9.—*Selenops kikay* new species. 6, Left palp, ventral view; 7, Left palp, detail of tibial apophysis; 8, Epigynum, ventral view; 9, Vulva. Scale = 0.20 mm.

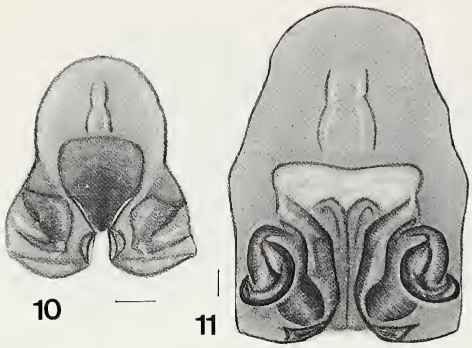


Figure 10, 11.—***Selenops para*** new species. 10, Epigynum, ventral view; 11, Vulva. Scale = 0.20 mm.

Diagnosis.—Males can be distinguished from those of all other selenopids by the presence of grooves in the retrolateral tibial apophysis and a large keel ending in three teeth (Fig. 7), and by a spatulate prolateral tibial apophysis with rounded lateral projection (Fig. 6); females by having the epigynum twice as long as wide, a small, subtriangular middle field (Fig. 8), and elongated heavily sclerotized spermathecae (Fig. 9).

Male.—Total length 7.55. Carapace 3.65 long, 4.15 wide. *Eye sizes and interdistances:* AME 0.23, ALE 0.13, PME 0.18, PLE 0.25, AME-AME 0.28, AME-ALE 0.43, AME-PME 0.13, PME-PME 0.83 PME-PLE 0.40, PME-ALE 0.33, PLE-PLE 1.65, ALE-ALE 1.55. Abdomen 3.90 long, 2.95 wide. Leg formula 2314. *Leg lengths:* I– femora 5.70, patellae + tibiae 7.30, metatarsi 4.90, tarsi 2.30, total 20.20, II– 6.70, 8.30, 5.30, 2.40, total 22.70; III– 6.80, 8.30, 5.10, 2.00, total 22.20; IV– 6.30, 6.60, 5.00, 2.10, total 20.00. *Leg spination:* femora I–IV p1–1–1, d1–1–1, r0–1–2; tibiae I–II p1–1–0, d1–1–0, r1–1–0, v2–2–2, III–IV p1–1–0, r1–0–0, v2–2–0; metatarsi I–IV p1–1–0, r1–1–0, v2–2–0. Carapace pale brown. Chelicerae pale brown with prolateral gray band. Legs brown. Femora I–II with ventral and longitudinal gray band, patellae I–IV with prolateral gray dark spots, tibiae I–IV with two incomplete pale gray rings, metatarsi IV dark brown. Abdomen pale gray-brown with central dark band at middle part, united with two diamond-shaped dark brown spots. Palp of male as in Figs. 6, 7.

Female.—Total length 10.25. Carapace 4.75 long, 5.20 wide. *Eye sizes and interdistances:* AME 0.30, ALE 0.15, PME 0.30, PLE 0.40, AME-AME 0.28, AME-ALE 0.55, AME-PME 0.08, PME-PME 0.90, PME-PLE 0.43, PME-ALE 0.23, PLE-PLE 2.08, ALE-ALE 1.88. Abdomen 5.50 long, 4.40 wide. *Note:* legs of paratype loose in vial. Coloration as in male. Epigynum and vulva as in Figs. 8, 9.

Other material examined.—**BRAZIL:** *Amazonas*: Manaus, Reserva Ducke, 4 January 1993, A. Brescovit, 1♂ (MCN 25526).

Distribution.—Bahía and Amazonas, Brazil.

Selenops para new species
Figs. 10, 11

Types.—Female holotype and paratype from Fátima de Uricurituba, Santarém, Pará, Brazil (24 January 1994, A. Brescovit), deposited in MCN, N° 25027.

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—*Selenops para* seems closest to *S. isopoda* Mello-Leitão, but females can be distinguished by the epigynal shape, with two longitudinal grooves in front of the subpentagonal middle field (Fig. 10), and by the form of the spermathecae (Fig. 11).

Female.—Total length 8.70. Carapace 3.00 long, 3.60 wide. *Eye sizes and interdistances:* AME 0.35, ALE 0.20, PME 0.40, PLE 0.45, AME-AME 0.18, AME-ALE 0.35, AME-PME 0.50, PME-PME 0.63, PME-PLE 0.28, PME-ALE 0.13, PLE-PLE 1.40, ALE-ALE 1.22. Abdomen 5.70 long, 4.30 wide. Leg formula 2341. *Leg lengths:* I– femora 3.50, patellae + tibiae 4.40, metatarsi 2.50, tarsi 1.20, total 11.60, II– 4.20, 5.10, 2.70, 1.20, total 13.20; III– 4.40, 4.80, 2.60, 1.20, total 13.00; IV– 4.00, 4.10, 2.50, 1.20, total 11.80. *Leg spination:* femora I p1–1–0, d1–1–1; II–IV d1–1–1; tibiae I–II v2–2–2, III–IV v1–1–0; metatarsi I–II v2–2–0, III–IV 1–1–0. Carapace pale orange-brown. Chelicerae pale brown with terminal gray band. Legs yellowish with gray spots. Femora I with two prolateral and distal little spots, tibiae I–IV some spots except on ventral part, metatarsi I–IV brown with thin retrolateral band distally, tarsi I–IV with three retrolateral black spots. Abdomen pale yellow with central and longitudinal pale brown band. Posterior portion of abdomen with lateral tufts of white hairs. Epigynum and spermathecae as in Figs. 10–11.

Male.—Unknown.

Material examined.—Only the types.

Distribution.—Known only from the type locality.

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RESEARCH NOTE

THE EXTREMELY RARE *PRODIDOMUS RUFUS* HENTZ (ARANEAE, PRODIDOMIDAE) IN CALIFORNIA

Recently, in southern California, I collected a mature male of *Prodidomus rufus* Hentz 1847; this is an extremely rare find. The family was erected by Hentz based on an immature *P. rufus* from Alabama (Hentz 1847, 1875); no additional mention of this spider was made until Banks (1892) collected several more immature specimens from Louisiana. It was many years later before the first mature female (Bryant 1935) and mature male (Bryant 1949) were described, both specimens being collected in Texas. When the subfamily Prodidominae was reviewed by Cooke (1964), these two specimens were the only known mature *P. rufus* spiders. Although members of the subfamily Prodidominae are distributed worldwide, they are sparsely represented in collections. In Cooke's review of 11 genera and approximately 40 species, he states "remarkably few specimens of this family have been collected, probably less than 200 individuals". Inquiries made to major North American collections, as well as to several arachnologists in the southern US, revealed few mature specimens of *P. rufus*. Other than the mature specimens described by Bryant, only one other mature male from Cuba has been collected (Alayon Garcia 1992) and only three mature females are known: two from California and one from Texas (N. Platnick pers. comm.)

A mature *P. rufus* male was collected on 27 May 1995 at 2200 h in Riverside, California (*Riverside County:* ¼ mi. W Sycamore Canyon Park (R. S. Vetter)) as it was actively moving about. The remarkable securing of this rare spider was juxtaposed by the banality of the collection locale: the bathroom countertop in the author's second-story apartment. This male agrees with the one described in Bryant (1949) with a few minor variations in somatic features. The Texas male is 3 mm long whereas this recently collected male is 4.5 mm in overall length (not including the chelicerae). Measurements for the Riverside specimen which are commensurate with those taken by Bryant (1949) are: cephalothorax (2.0 mm long, 1.5 mm wide), abdomen (2.5 mm long, 1.7 mm wide) and palpus (2.5 mm long).

Two mature female *P. rufus* (previously unreported) have also been found in California: *Imperial County:* (1 mi. W Harper's Well, San Felipe Creek, 7 November 1968 (M. E. Irwin, P. A. Roach)). *Kings County:* (Kettleman Hills, 4 February 1994, under rocks and boards (W. H. Tyson)). Although the predominant pantropic habitat for *Prodidomus* is hot, dry desert, some species have been collected in damp forest (Cooke 1964). The most common collection site for several species is from underneath rocks while others are synanthropic with the dubious habitat of the African *P. domesticus* Lessert 1938 given as "leper's huts" (Cooke 1964). Regarding this most recently collected *P. rufus*, the landscaping of the Riverside collection site consists of an abundance of tall broad-leafed trees (eucalyptus, sycamore, alder) and grassy areas with the neighboring property being other apartment complexes and a chaparral-dominated xeric natural park. The majority of synanthropic spiders collected inside the author's domicile have consisted of gnaphosids, clubionids and pholcids.

In the past, the Prodidomidae has been associated taxonomically with the Gnaphosidae due to gross morphological similarities (i.e., enlarged, well-separated spinnerets) but was revalidated to family rank by Platnick (1990)

based on more refined spinneret spigot morphology. The eye pattern almost creates a circle due to the extremely procurved nature of the posterior eye row intersecting with the straight anterior eyes. The AME of most prodidomids are darkly pigmented whereas the other six eyes are not. Other characteristics that help distinguish this spider are protruding, geniculate chelicerae and unarmed tarsal claws.

Of the three known California *P. rufus*, the Kings County specimen is housed in the California Department of Food & Agriculture collection (Sacramento); the other two specimens are in the Univ. of California, Riverside Entomology Museum Collection. I would like to thank Dr. N. Platnick for supplying information, for corroborating my identification and for making comments on a draft of the manuscript. S. Frommer and W. Icenogle also made helpful comments, and W. Poehner translated the paper in *Poeyana*. I thank the following for responding to my inquiries of the occurrence of *P. rufus* in collections of their museums and/or states: R. Breene, A. Dean, G. B. Edwards, C. Griswold, W. Icenogle, D. Richman, P. Sierwald.

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Note added in proof: Despite the apparent rarity of this spider, with great astonishment, I collected yet another specimen of *P. rufus,* once again inside my apartment. On 19 February 1996 (2100 h during rainy weather), a mature female was discovered on a dining room wall, four m from where the male was found. This spider (the fifth known mature female ever collected) is 6.2 mm long with a 2.5 mm cephalothorax and 3.7 mm abdomen. In alcohol, the unpigmented eyes in both Riverside specimens form a contiguous band of silver. The female was viewed alive; and the nonpigmented eyes were separated by discrete distances and carapace pigmentation, looking very much like a typical gnaphosid. Because my only previous experience with this species was the preserved male, I did not recognize the significance of my catch until the female was preserved; otherwise, it would have been kept alive to obtain life history information of which there is virtually none for the whole family. Identification was corroborated by N. Platnick, the spider is housed in the University of California, Riverside collection; and I remain bemused why my abode has become a hospice for this very rare species.

1996. The Journal of Arachnology 24:74–75

RESEARCH NOTE

ANOTHER PSEUDOSCORPION FROM EMPIRE CAVE, SANTA CRUZ COUNTY, CALIFORNIA (CHTHONIIDAE)

The pseudoscorpion *Fissilicreagris imperialis* (Muchmore) is currently being proposed as a candidate for listing as an endangered or threatened species because its habitat—Empire Cave and other caves in Cave Gulch, Santa Cruz County, California—is seriously threatened by vandalism and development (see Muchmore & Cokendolpher 1995). Another unique, heretofore undescribed, pseudoscorpion also lives in Empire Cave. As it, too, is threatened, it is described below to allow the recognition it deserves.

Genus *Neochthonius* Chamberlin

Neochthonius Chamberlin 1929:66; Muchmore 1969:388; Judson 1990:593–594.

Type species *Neochthonius stanfordianus* Chamberlin 1929, by original designation.

Neochthonius imperialis new species
(Fig. 1)

Type data.—Holotype. Female (WM7720.01001), from Empire Cave, Cave Gulch, Santa Cruz County, California, 8 September 1991, D. Ubick and S. Fend; mounted on slide, in California Academy of Sciences, San Francisco, California.

Diagnosis.—Similar to *Neochthonius stanfordianus* Chamberlin, but larger (palpal femur length 0.54 versus 0.39–0.43) and without eyes (versus two eyes).

Description of female (male unknown).—With the characters of the genus *Neochthonius* (see Muchmore 1969) and the following particular features. Palps and chelicerae light brown, carapace and other parts tan. Carapace slightly longer than broad; epistome distinct, serrate; no eyes; chaetotaxy 6-4-4-2-2. Coxal chaetotaxy 2-2-1: mmm2(3)-0: 2-2-CS: 2-4-CS: 2-4; each coxa II with four bipinnate coxal spines (CS) arranged in a row, each coxa III with three similar spines. Tergal chaetotaxy 4:4:4:4:6:6:6:6:6:4:1T2T1:0; sternal chaetotaxy 12:(3)10(3):(2)7(2):m5m:m5m:m5m:?:?:7:0:2. Chelicera nearly as long as carapace; hand with six setae; flagellum of about eight setae; galea a small knob. Palp moderately slender (Fig. 1): L/B of trochanter 2.0, femur 4.9, patella 1.95, and chela 4.75; L/D of hand 1.8; movable finger L/hand L 1.85. Trichobothria typical. Fixed finger with 68 tall, cusped, retrorse teeth; movable finger with 52 mostly retrorse teeth. Leg IV with L/D of femur + patella 2.3 and tibia 3.75.

Measurements (mm).—Body L 1.38. Carapace L 0.46. Chelicera L 0.445. *Palp:* trochanter 0.21/0.105; femur 0.54/0.11; patella 0.245/0.125; chela 0.805/0.17; hand 0.29/0.16; movable finger L 0.54. *Leg IV*: femur + patella 0.415/0.18; tibia 0.28/0.075; basitarsus 0.15/0.06; telotarsus 0.42/0.04.

Etymology.—The species is named *imperialis* after its type locality, Empire Cave.

Remarks.—*Neochthonius imperialis* is found within the geographic range of *N. stanfordianus* (see Schuster 1962), from which it differs in being larger and eyeless. It is close in size and proportions to *N. amplus* (Schuster), which is distributed north of San Francisco, on the east side of the Coast Range; from this species it is distinguished by the complete loss of eyes, undoubtedly an adaptation to life in the cave. It is much smaller and less slender than the only other known cavernicolous species in the genus, *N. troglodytes* Muchmore, from Wool Hollow Cave, Calaveras County.

The type locality, Empire Cave, is also the type locality of *Fissilicreagris imperialis* (Muchmore), which has been found in two additional caves in Cave Gulch (see Muchmore

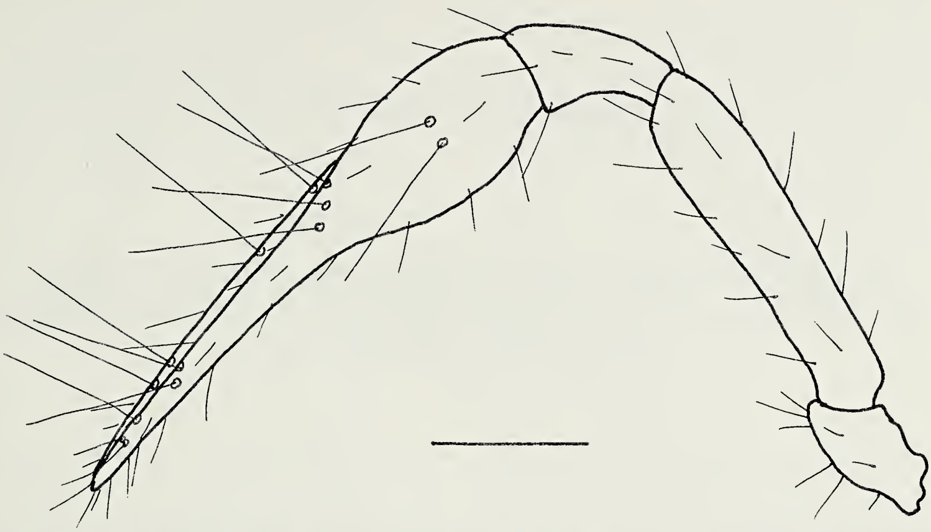

Figure 1.—**Neochthonius imperialis** new species, holotype. Right palp, dorsal view. Scale line = 0.2 mm.

& Cokendolpher 1995). It is quite possible that *Neochthonius imperialis*, too, has a wider distribution than the one cave, but has been overlooked because of its much smaller size. If it, also, is unique to the small Cave Gulch karst area, then it deserves to be on the list of endangered or threatened species, along with *F. imperialis*.

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RESEARCH NOTE

WOLF SPIDERS VARY PATCH RESIDENCE TIME IN THE PRESENCE OF CHEMICAL CUES FROM PREY (ARANEAE, LYCOSIDAE)

Foraging efficiency of 'sit-and-wait' predators is an important influence on animal fitness (Stephens & Krebs 1986). It is suggested that the decision of how long to stay in a foraging patch before moving to another (patch residence time) will affect energy intake rates and may contribute to fitness (Morse & Fritz 1982).

Many studies have sought to identify the proximal cues spiders use to determine both the choice of foraging patches (Kronk & Riechert 1979; Cady 1984; Morse & Fritz 1982; Riechert 1985; Riechert & Gillespie 1986; Morse 1993; Pasquet et al. 1994) and the duration of time spent in a patch (Turnbull 1964; Janetos 1982; Greenstone 1983). Both environmental factors such as temperature (Riechert 1985), humidity (Cady 1984), and vegetation structure (Morse & Fritz 1982; Lesar & Unzicker 1978) as well as factors that relate to prey abundance (Turnbull 1964; Riechert 1976; Gillespie 1981), hunger (Turnbull 1964; Wise 1975), and perceptual cues (Lizotte & Rovner 1988; Morse 1993; Persons & Uetz in press) have been shown to affect patch choice and/or residence time.

Chemical cues, although well-known to be important components of courtship communication for many species of wolf spiders (Kaston 1936; Hegdekar & Dondale 1969; Tietjen 1979; Rovner 1991), have never been demonstrated to be an important component of foraging decisions with respect to patch residence time. The presence of chemosensory hairs on the male pedipalps has been mapped and related to microhabitat preferences of spiders (Tietjen & Rovner 1980). Some experiments have demonstrated that male *Schizocosa saltatrix* (Hentz 1844) and *S. ocreata* (Hentz 1844) may be capable of responding to airborne pheromones (Tietjen 1979). Whether or not spiders use chemical cues within a foraging context is not known. The data presented here examine whether adult female *S. ocreata* use the substratum-borne chemical cues of prey to modify the duration of time spent in a foraging patch.

Twenty immature female *S. ocreata* wolf spiders were caught in September of 1994 at the Cincinnati Nature Center, Clermont County, Ohio. Each spider was housed in its own container, provided water *ad libitum*, and fed three one-week old crickets every four days to standardize hunger level for testing. Spiders were allowed to mature while being maintained on a plaster of Paris substratum at room temperature (23–25 °C) and stable humidity with a 12:12 L:D photoperiod.

Two differently treated substrata were compared for effects on patch residence time; each substratum consisted of a sheet of copy paper 20 cm in diameter. For the experimental treatment, 100 one-week old crickets were allowed to walk on the paper for a 30 min interval. For the control treatment, a clean sheet of paper was used.

The test apparatus consisted of two containers made of white foam-core board. Each container housed two round chambers (Fig. 1). One chamber served as a neutral chamber into which the spider was introduced, and the other chamber contained either the control paper or the substratum that crickets walked upon. Each spider was tested under both treatments in random order.

An experimental trial consisted of a single spider introduced into the neutral (no test substratum) chamber under a clear plastic vial.

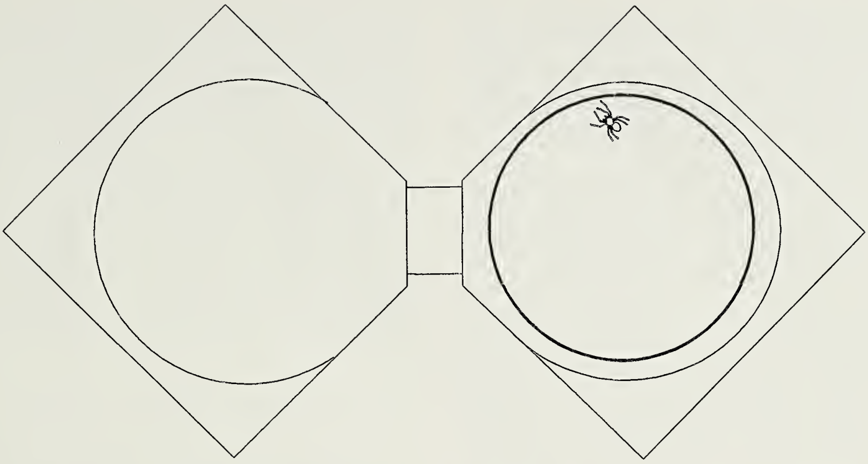

Figure 1.—The artificial foraging environment used for spider testing. Each apparatus consists of two chambers: a neutral chamber and a chemical stimulus chamber. The stimulus chamber contains a circular disk that is either permeated with prey-produced chemical stimuli or serves as a control disk without such stimuli. Spiders are placed in the 'neutral' chamber prior to each experiment (spider shown in stimulus chamber) and allowed to move freely between the two chambers after a five minute acclimation period.

After a five min acclimation period, the vial was removed and the spider was allowed to enter and exit the single treatment chamber freely for a 30 min time period. Each trial was videotaped from above and duration and number of chamber visits was determined by videotape analysis. A new paper disk was used for each 30 min trial to reduce any effect produced by draglines of previous spiders introduced to the chambers.

The final visit into a treatment chamber was

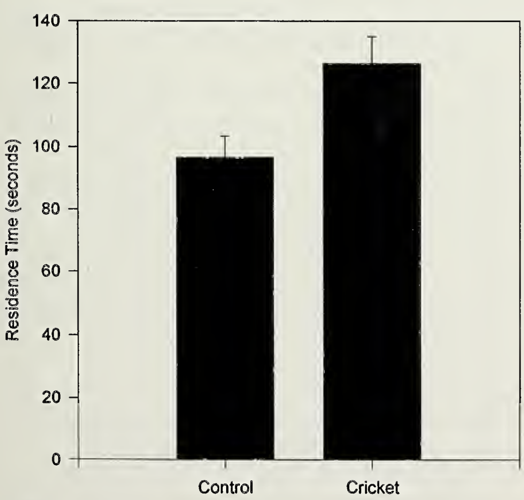

Figure 2.—Mean patch residence times (±SE) by cricket chemical cue stimulus. (n = 20).

omitted if the spider was in the chamber when the trial time had expired. All 20 spiders visited each treatment chamber at least three times and were used in the analysis.

Before analysis, patch residence time was natural log (ln) transformed to conform to ANOVA assumptions of normality. A fully crossed mixed model two-way ANOVA was used to analyze the variation in duration of patch visits. Patch residence time was tested using individual spider (random effect) and substratum-cue (fixed effect) as factors. F-values were adjusted using the appropriate mean squares ratio for a mixed model design.

Spiders spent significantly longer periods of time on substrata that crickets had walked on previously (mean = 126.2 sec; SE = 8.59) over substrata that lacked prey chemical cues (adjusted $F_{1, 19}$ = 13.31; 0.001 < P < 0.005) (mean = 96.4 sec; SE = 6.86) (Fig. 2). There were significant differences between individual spiders with respect to patch residence time ($F_{19, 302}$ = 6.29; P < 0.001), but no significant interaction between individual spiders and substratum type ($F_{19, 302}$ = 1.29; P > 0.05).

These wolf spiders have the ability to perceive chemicals left by prey. Although the video recording did not allow for close study of the precise behavioral responses to the chemical cues, it was apparent that the high

turning rates typically observed by male spiders chemo-exploring in the presence of female pheromones was lacking. The primary observable difference was in the proportion of time the spider was stationary under the two treatments.

It is unclear what chemicals the spiders are using as a cue or what chemosensory organs are involved. Studies by Harris & Mill (1977) have found that dictynid spiders have curved, blunt-tipped chemosensory hairs that are capable of perceiving various halide salts and acids but have little response to amino acids, urea or some sugars. Stimuli from fly and beetle extracts also failed to elicit a response. Similar chemosensory hairs have been identified and mapped on the palps of several species of wolf spider (Tietjen & Rovner 1980; Kronestedt 1979; Foelix & Chu-Wang 1973). These studies suggest that the pedipalps may be a possible site for perceiving chemical cues, although they may be quite specific in their responses. These experiments have focused primarily on male chemosensory organs with less emphasis of female chemosensory hairs. This study suggests that female wolf spiders may use chemical cues as a source of information while foraging in addition to visual and vibratory information from prey (Lizotte & Rovner 1988; Persons & Uetz in press).

Caution is indicated in the interpretation of these data, as the mean difference between time spent on the chemical cues substratum versus the control was not large. This, combined with the high numbers of crickets used for the experimental treatment, raises questions about to what degree spiders use chemical cues in a natural setting. It is known that spiders use chemical cues in the rejection of unpalatable prey (Givens 1978; Vasconcellos-Neto & Lewinsohn 1984), but research presented here suggests that chemical information may provide a valuable source of information for making patch residence time decisions as well.

ACKNOWLEDGMENTS

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The American Arachnological Society Fund for Arachnological Research (AAS Fund) is funded and administered by the American Arachnological Society. The purpose of the fund is to provide research support for work relating to any aspect of the behavior, ecology, physiology, evolution, and systematics of any of the arachnid groups. Awards may be used for field work, museum research (including travel), expendable supplies, identification of specimens, and/or for preparation of figures and drawings for publication. Monies from the fund are not designed to augment or replace salary. Individual awards will not normally exceed $500.00, and preference will be given to students over part-time or tenured faculty. Up to five research awards will be made during each Winter-Spring or Summer-Fall granting period. Applications for support should be received by the chair of the review committee no later than May 30 or November 30, for funding by June 30 and December 30, respectively.

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Figures 1–4.—*A-us x-us,* male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us,* holotype male; 33, 34, *A-us y-us,* male. Scale = 1.0 mm.

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Research Notes

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THE JOURNAL OF ARACHNOLOGY

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Cover illustration: Carving of a pseudoscorpion on the bottom of hand-decorated dried gourd bowl from Maroua, Province d'Extreme Nord, Cameroon. Photo by James C. Cokendolpher.

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STUDIES ON THE SYSTEMATICS AND DISTRIBUTION OF THE SCORPION *VAEJOVIS BILINEATUS* POCOCK (VAEJOVIDAE)

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ABSTRACT. A revised diagnosis is given for the scorpion *Vaejovis bilineatus* Pocock, a member of the *eusthenura* group, based on newer characters of taxonomic importance. New distributional records presented herein expand the known range of the species to cover much of northeastern Mexico, specifically the states of Coahuila, Nuevo León, Tamaulipas, Aguascalientes, Guanajuato, and San Luis Potosí. The results of an analysis of character variation involving coloration, pectinal tooth counts, pedipalp chela finger dentition, trichobothrial patterns, morphometrics, and setal counts of the pedipalps and metasoma are also provided.

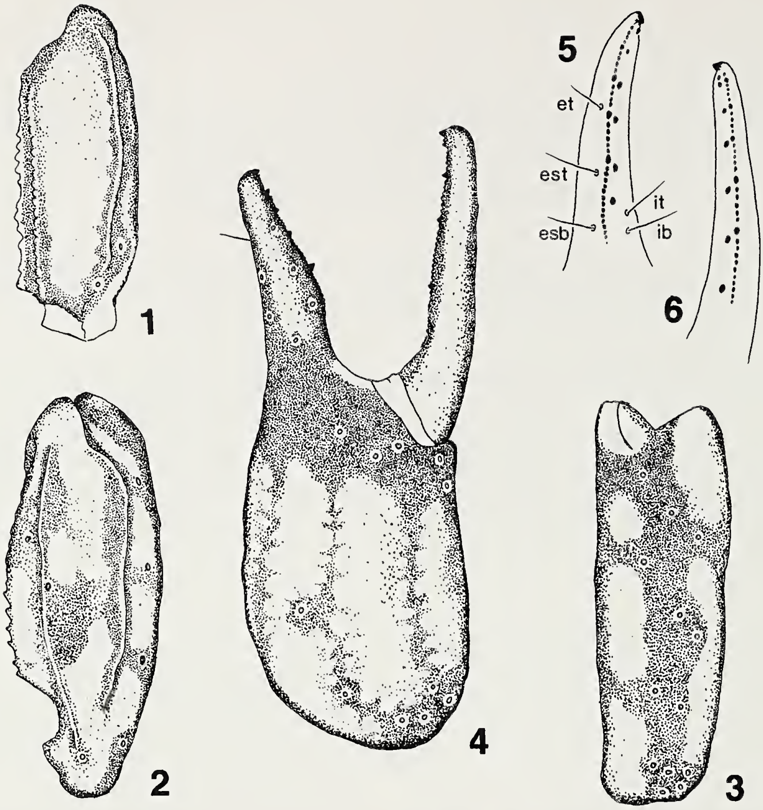
The scorpion *Vaejovis bilineatus* Pocock was described in 1898 on the basis of a single female specimen that supposedly originated from San Diego, Texas (Pocock 1898). Kraepelin (1899) regarded *V. bilineatus* as a variant of *Vaejovis spinigerus* (Wood), but this view was overturned by Hoffmann (1931), who recognized *V. bilineatus* once again as a valid species. Hoffmann somewhat tentatively referred his 20 specimens from Tepezala, Aquascalientes, Mexico to this species because they closely matched the original description. The type specimen of *V. bilineatus* was subsequently studied and redescribed by Williams (1970), and that author accepted Hoffmann's specimens as *V. bilineatus*, based on comparison of the holotype to Hoffmann's detailed description. Our findings, based on reexamination of some of Hoffmann's specimens, are in full agreement with those of Williams.

The distribution of *V. bilineatus* has remained poorly understood. Although the fauna of southern Texas is fairly well known, *Vaejovis bilineatus* has not been collected in the state subsequent to the original description. It is likely, therefore, that the holotype was mislabeled, and its locality data are erroneous. Díaz Nájera (1975) listed a single new record for Coronea, Guanajuato and Sissom & Francke (1983), in a life history study of the species, reported a new record for Villa Hidalgo, San Luis Potosí. Díaz Nájera's specimens were not examined and his record, which lies far to the south, will probably require subsequent confirmation. Consequently, after nearly 100 years there are only two or three published localities for *V. bilineatus* that can be considered accurate.

Since these earlier studies, a number of new specimens have accumulated in various museum collections, particularly the American Museum of Natural History (AMNH) in New York, the Texas Memorial Museum (TMM) in Austin, and Museum of Zoology at Louisiana State University. The latter specimens are now deposited in the Florida State Collection of Arthropods (FSCA) in Gainesville. These new specimens allowed us to update the diagnosis for the species based on taxonomic characters recently found important, describe in good detail the geographical distribution of the species, and analyze variation in color, morphometrics, and meristics. Morphometric characters are derived from measurements of 12 adult males and 12 females; for other characters studied, almost all adult and late instar juvenile specimens available were utilized. All measurements were taken using an ocular micrometer calibrated at 20×.

Vaejovis bilineatus Pocock
(Figs. 1–21)

Vaejovis bilineatus Pocock 1898:395; *nec* Gertsch 1939:18 (misidentification, = *V. waueri* Gertsch & Soleglad 1972); Gertsch & Soleglad 1972:605; Stahnke 1974:135; Díaz Nájera 1975:6, 8, 22;



Figures 1–6.—Morphology of *Vaejovis bilineatus*, male from Villa Hidalgo, San Luis Potosí. 1, Pedipalp femur, dorsal aspect; 2, Pedipalp patella, dorsal aspect; 3, Pedipalp patella, external aspect; 4, Pedipalp chela, external (lateral) aspect; 5, Pedipalp chela fixed finger, showing dentition and trichobothrial pattern; 6, Pedipalp chela movable finger, showing dentition. Trichobothrial designations for Fig. 5 are as follows (after Vachon 1974): *esb* = external subbasal; *est* = external subterminal; *et* = external terminal; *ib* = internal basal; *it* = internal terminal.

Sissom & Francke 1983:69–75; Francke & Sissom 1984:17, tables 6, 7.

Vaejovis spinigerus var. *bilineata* Kraepelin 1899: 187.

Vejovis bilineatus Hoffmann 1931:347 (key), 362–364, fig. 26; Williams 1970:238–241, figs. 1, 2.

Description.—Adults 22–32 mm in length. Base color yellow brown; carapace with dark underlying pattern; mesosomal dorsum usually with one pair of moderately dark, longitudinal submedian stripes (in some populations there are dark lateral blotches on each tergite as well); metasoma with variable mottling on dorsal and lateral faces and with ventral submedian and ventrolateral carinae underlined in dark pigment; metasomal segment V and sometimes IV slightly darker than preceding segments, particularly on underside. Carapace with anterior margin more or less straight, but with small median notch. Sternite VII with carinae obsolete. Pectinal tooth counts 15–19 in males and 14–16 in females. *Metasoma:* Segments I–III wider than long, V 2.00–2.38 times longer than wide in males, 1.78–2.18 times longer than wide in females; ventral submedian carinae on I–IV obsolete, sometimes weak, crenulate on IV; ventrolaterals on I–IV moderate, smooth to crenulate. *Pedipalps:* Femur tetracarinate with carinae of dorsal surface moderate, crenulate (Fig. 1); patella (Figs. 2, 3) with dorsointernal and dorsoexternal carinae weak, smooth to granular in males and faint, smooth in females; inner face moderately convex, with inner keel granular in males, smooth to granular in females. Chela (Fig. 4) with all carinae essentially obsolete; chela fixed finger (Fig. 5) with primary denticle row divided into five sub-rows; mov-

able finger (Fig. 6) with primary row divided into six sub-rows (including the apical sub-row containing a single small denticle); male palm slightly swollen, female palm slender; cutting margins of male chela fingers moderately scalloped, female fingers with cutting margins straight. Pedipalp chela length/width ratio, 2.81–3.55 in males, 3.37–4.00 in females; pedipalp femur length/carapace length ratio, 0.67–0.73 in both sexes; pedipalp patella length/width ratio, 2.22–2.64 in both sexes; chela fixed finger length/carapace length ratio, 0.48–0.55 in both sexes; chela movable finger length/chela width ratio, 1.58–2.0 in males, 2.03–2.38 in females; chela movable finger length/metasoma V length ratio, 0.54–0.61 in males, 0.62–0.68 in females. Trichobothria *ib* and *it* situated near the sixth (basalmost) inner accessory denticle of fixed finger denticle row, usually with *it* at the level of or slightly basal to the denticle.

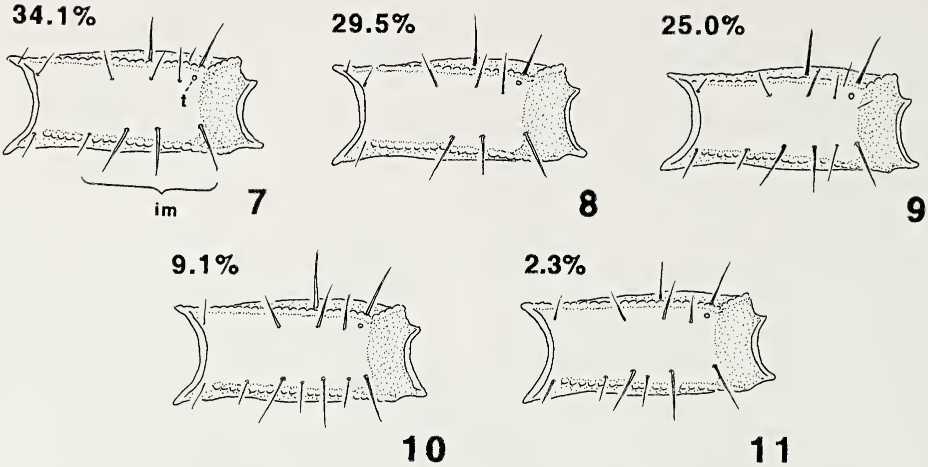
Specimens examined (all from Mexico).—*Aguascalientes*: 2 mi W Asientos (7300 ft.), 9 June 1956 (B. Banta), 2♂, 1♀ with 19 1st instar young (AMNH); Tepezala, no date (C. C. Hoffmann), 4♂4♀ (AMNH–C. C. Hoffmann Collection). *Coahuila:* 5.4 mi W Bunuelos in Valle de Guerra, 15 July 1977 (E. A. Liner, Chaney), 2♀ (FSCA). *Nuevo León:* 4.5 mi N La Ascension, 19 July 1975 (E. A. Liner), 2♀ + 9 1st instar young (FSCA); 6.9 mi W El Carmen, 15 July 1976 (E. A. Liner, et al.), 1♀ (FSCA); 2.7 mi N, 2.4 mi SE La Ascension on La Caballada Road, 19 July 1975 (E. A. Liner, et al.), 2♂3♀ (FSCA); 7.7 mi N La Ascension, 19 July 1975 (E. A. Liner), 2♂1♀ (FSCA); 3 km S San Roberto (under cactus), 13 Aug 1972 (N. V. Horner), 1♀ (WDS). *San Luis Potosí:* 22 mi S Huizache, 20 Sept 1979 (J. C. & J. E. Cokendolpher), 1♂ (WDS); KM 20 on Hwy 70, March 1972 (collector unknown), 2♂1♀1juv. (AMNH); 40 mi W Valles, March 1972 (collector unknown), 1♀2juv. (AMNH); Hwy 70, 70 mi W Valles, 19 February 1970 (J. A. L. Cooke, R. W. Mitchell), 1♂2♀1juv. (AMNH), 1♂1♀ (WDS); near Ciudad del Maiz, 19 Aug 1947 (C. & M. Goodnight), 1♀ (AMNH); km 50 on Hwy 57, 18 Mar 1972 (J. M. Rowland), 1♂ (TMM); San Luis Potosi (in or near city?), no date (H. F. Wickham), 1♂ (USNM). *Tamaulipas:* km 14 on Hwy 101, 22 Feb 1973 (W. Graham, T. R. Mollhagen, C. McConnell), 3♂8♀2juv. in three vials (AMNH); km 53 on Hwy 101, 23 Feb 1973 (T. R. Mollhagen), 1 subadult♂1♀ (AMNH); km 92 on Hwy 101, 22 Feb 1973 (T. R. Mollhagen) 1♂8♀ (AMNH); km 15 on Hwy 19, 18 Mar 1972 (J. A. L. Cooke), 1♀ (AMNH); 4 mi N Juamave, 20 Sept 1979 (J. C. & J. E. Cokendolpher), 1♀ (WDS); Ciudad Victoria, June 1977 (F. D. White), 1♀ (WDS); 1 km NW La Presita, 20 Sept 1979 (J. C. & J. E. Cokendolpher), 2♀ (WDS); Palmillas, "12–3–64" (T. Raines), 2♀ (AMNH). *State uncertain*: Gonzalez (= Villa González Ortega, Zacatecas?), no date (H. F. Wickham), 2♀ (USNM).

CHARACTER ANALYSIS

Color pattern.—There was considerable variation observed in color pattern, so much so that the name "*bilineatus*" now seems inappropriate. Specimens in some parts of the range, particularly in Tamaulipas and eastern San Luis Potosí, bore not only the distinctive submedian stripes, but also had dark blotches near the lateral edges of the tergites. This gave the scorpions the appearance of having four dorsal stripes rather than two. The variation in color pattern suggested the possible presence of two species; however, the search for additional characters that could consistently distinguish the two color forms was not productive. Further, in the southern part of the range (southwestern San Luis Potosí) specimens were intermediate in color pattern, with diffuse lateral blotches that were essentially continuous with the median stripes. One interesting feature in specimens from eastern San Luis Potosí (those also bearing four dorsal stripes) was a general tendency for the males to have crenulated ventrolateral metasomal carinae on segments I–IV and crenulated ventral submedian carinae on segment IV. However, typical two-striped males in other parts of the range occasionally had weak crenulations on the ventrolateral carinae as well. Consequently, it seems best at this time to regard the color variation as intraspecific in nature.

Pectinal tooth counts.—Pectinal tooth counts varied in the specimens examined as follows (damaged combs were not counted): in males, there were 3 combs with 15 teeth, 21 combs with 16 teeth, 22 combs with 17 teeth, 1 comb with 18 teeth, and 2 combs with 19 teeth; in females, there were 9 combs with 14 teeth, 41 combs with 15 teeth, and 16 combs with 16 teeth. There was no discernible geographical pattern in pectinal tooth count variation.

Pedipalpal macrosetal counts.—Haradon (1983, 1984a, 1984b, 1985), in his revisionary work on the genus *Paruroctonus* Werner, found the numbers and distribution of pedipalpal macrochaetes to provide good specific



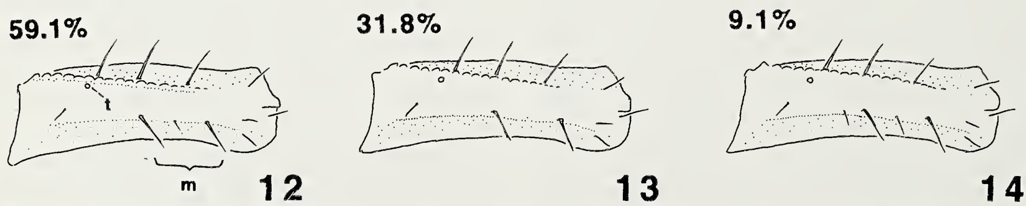
Figures 7–11.—Variation in setation of the internal (anterior) face of the pedipalp femur in *Vaejovis bilineatus*. Percentages represent the proportion of specimens (n = 44) that bore the particular setal pattern. Designations are as follows: t = trichobothrium; *im* = inframedial setae.

characters. It is worthwhile, as Haradon suggested, to investigate these characters in other vaejovids, so we conducted a thorough analysis on our specimens of *V. bilineatus*. Our findings indicated that the setal characters exhibited high intraspecific variation that was not geographically based. The patterns of the femoral and patellar setae are described and illustrated below; the frequency of occurrence of each pattern is provided with its illustration.

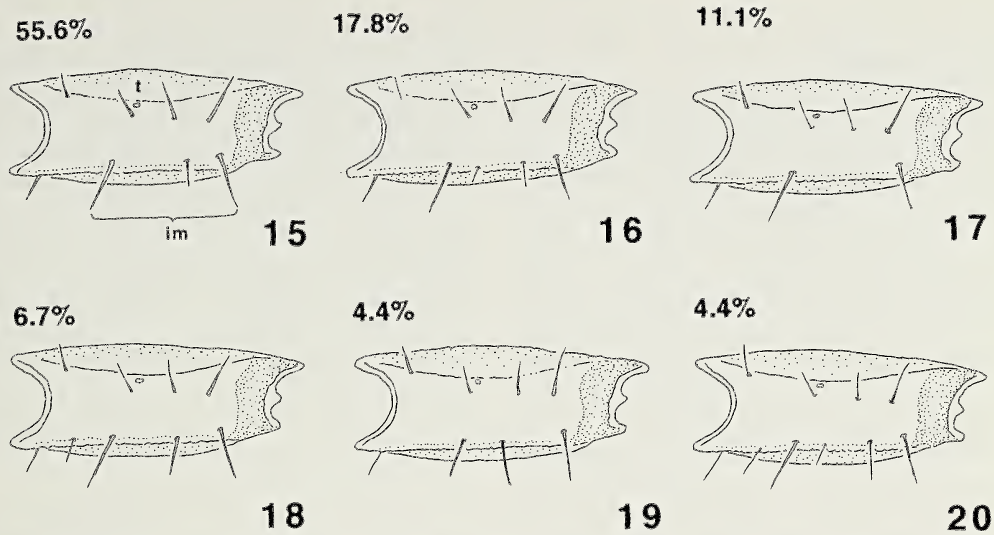
For the inframedial setae of the inner face of the pedipalp femur, five relatively distinct setal patterns were identified (Figs. 7–11), three of which were prevalent. In each pattern, there were three larger setae evenly spaced from the base of the femur; in addition, there were variable numbers of smaller setae (none, one, two, or three). These smaller setae were usually directly in the row, but in some cases were positioned closer to the ventrointernal carina. There were also instances where the setae were so small that, in our judgment and according to Haradon's definition, they should not have been classified as macrosetae. In such cases, the setae were not counted.

Another set of diagnostic setae was the medial series of the external face of the femur (Figs. 12–14). As shown in the figures, three distinct patterns were observed. In each, there were two major setae. Usually, in between the two major setae was another smaller seta that was quite variable in size. In many cases this seta was missing, as evidenced by a tiny socket. Based on the size of the socket, the specimen was more or less arbitrarily assigned to either the first (Fig. 12) or second setal pattern (Fig. 13). There were also cases in which no socket could be detected at all (Fig. 13) Finally, in a few specimens, a small seta occurred on the proximal side of the two majors (Fig. 14).

Six distinct patterns occurred for the inframedial setae of the internal face of the patella



Figures 12–14.—Variation in setation of the external (posterior) face of the pedipalp femur in *Vaejovis bilineatus*. Percentages represent the proportion of specimens (n = 44) that bore the particular setal pattern. Designations are as follows: t = trichobothrium; m = medial setae.



Figures 15–20.—Variation in setation of the internal (anterior) face of the pedipalp patella in *Vaejovis bilineatus*. Percentages represent the proportion of specimens (n = 45) that bore the particular setal pattern. Designations are as follows: t = trichobothrium; im = inframedial setae.

(Figs. 15–20). There were always two large, thick setae around which were interspersed variable numbers of smaller setae. The size of these smaller setae varied considerably from specimen to specimen—in some cases, they were quite short and thin and in others, relatively long and thick. In the latter case, they were almost as long as the two major setae, but were never as thick.

Tarsal setae.—Setae of the retrolateral aspect of tarsomere II (= telotarsus II) of the leg (leg III was utilized here) were consistent in number and position throughout the range of the species. There were two retrosuperior setae and two retromedials (see Haradon 1984 for explanation of terminology).

Metasomal setation.—Metasomal setation was highly variable, owing to the presence of numerous accessory setae of varying sizes on and between the keels (especially on the ventral surface). In many cases the setae were missing, leaving only the socket. Consequently, interpreting the pattern of pairing was sometimes subjective. The larger setae actually positioned on the carinae of 48 specimens were counted; segments in which the counts were questionable were not tallied in the results.

Setation of the dorsolateral carinae of segments I-IV: Only setae of the carinae of the left side were counted, and a modal count of 1:2:2:3 was obtained. Segment I had either one (70.8% of the specimens) or two (29.2%) setae; segment II had either one (4.3%), two (78.3%), three (10.9%), or four (6.5%) setae; segment III had either two (68.1%), three (23.4%), four (6.4%), or five (2.1%) setae; and segment IV had either two (21.3%), three (55.3%), four (14.9%), five (6.4%), or six (2.1%) setae.

Setation of the ventral submedian carinae of segments I-IV: Because the setae of the two keels were easily inspected simultaneously, they were counted on both sides. There was a modal setal count of 3/3:4/4:4/4:5/5 with variable numbers of accessory setae located between the carinae on each segment. Segment I was very uniform (91.3% of the specimens exhibited the modal count, with only a few specimens bearing four setae on one side or both); however, there was great variability on segments II–IV. For segment II, 25% of the specimens possessed a 3/3 count; 10.4% a 3/4 count; 37.5% a 4/4 count; 16.7% a 4/5 count; and 10.4% a 5/5 count. For segment III, 4.3% exhibited a 2/4 count; 8.7% a 3/3 count; 17.4% a 3/4 count; 30.4% a 4/4 count; 8.7% a 4/5 count; 6.5% a 4/6 count; 21.7% a 5/5 count; and 2.2% a 6/6 count. For segment IV, 5.0% possessed a 3/4 count; 15.0% a 4/4 count; 20.0% a 4/5 count; 2.5% a 4/6 count;

47.5% a 5/5 count; 5.0% a 5/6 count; and 5.0% a 6/6 count.

Setation of the dorsolateral and ventrolateral carinae of metasomal segment V: (left side only counted in both cases) The dorsolateral carina bore 7–12 setae, with nine (36.6%) and 10 (29.3%) being the most common numbers; lower percentages of specimens had eight (12.2%), 11 (9.8%), seven (7.2%), and 12 (4.9%). The ventrolateral carina bore 7–13 setae, again with 9 and 10 representing the most common observations (37.5 and 25.0%, respectively); all other setal counts occurred at frequencies of 10% or less.

Trichobothrial pattern.—Trichobothrial numbers tend not to vary in species of *Vaejovis* Koch, except for certain species in the *nitidulus* group (Sissom & Francke 1985), in which there is a single accessory trichobothrium on the external face of the pedipalp patella. Trichobothrial positions also tend to be relatively stable, although certain trichobothria may occur in locations that provide diagnostic characters for species groups. One important trichobothrial pair, *ib* and *it* on the chela fixed finger, varies in position from group to group. *Vaejovis bilineatus* seems most closely related to *V. waueri* Gerstch & Soleglad, *V. punctatus* Karsch, and *V. spinigerus* (Wood); the latter has been placed by Williams (1980) in the *eusthenura* group. In all members of the *eusthenura* group, *ib* and *it* are displaced distally from the base of the fixed finger to near the level of the sixth inner accessory denticle. As observed in *V. bilineatus*, slight variation does occur in the relative positions of these trichobothria. Trichobothrium *it* may occur at the level of the sixth inner accessory denticle or just proximal to it (Fig. 5); because *ib* is always a set distance from *it*, its position will vary accordingly.

Pedipalp chela finger dentition.—In all vaejovids except *Serradigitus* Stahnke, pedipalp chela finger dentition has been accepted as a very stable character. Much of the variation in the number of denticle sub-rows and inner accessory denticles appears to be due either to developmental anomalies or to injuries that were improperly repaired during molting. Only in *Serradigitus* spp. is significant 'normal' intraspecific variation in these characters observed.

Variation in chela finger dentition has never been quantified. Therefore, during the current study the right chela fingers of 46 specimens of *V. bilineatus* were analyzed. In 43 specimens (93.5%), the primary denticle row of the fixed finger was divided into five sub-rows by four enlarged primary row denticles (Fig. 5); in two specimens (4.3%) the denticle row was divided into four sub-rows by three enlarged denticles; and in one specimen (2.2%), the denticle row was divided into six sub-rows by five enlarged denticles. Forty-two (91.3%) of the specimens possessed six inner accessory denticles positioned medially alongside the primary denticle row of the fixed finger, whereas three specimens (6.5%) possessed five inner accessory denticles and one specimen (2.2%) possessed four.

In 42 of the specimens (91.3%), the movable finger bore six sub-rows: an apical sub-row of one denticle followed by five longer sub-rows (Fig. 6). In three specimens (6.5%), the apical sub-row was missing, leaving only the five main sub-rows, and in one specimen (2.2%) there were only four sub-rows. The number of inner accessory denticles of the movable finger varied as follows: 41 specimens (89.1%) had seven, two (4.3%) had six, one (2.2%) had five, one (2.2%) had eight, and one (2.2%) had 10. The specimen with eight inner accessory denticles had the extra one immediately next to the usual basalmost; the specimen with 10 had two extra denticles near the fingertip and the third at the basalmost position.

DISCUSSION

Vaejovis bilineatus is now known to exhibit a wide geographical distribution that includes at least six states in northern and central Mexico: Aguascalientes, Coahuila, Guanajuato, Nuevo León, San Luis Potosí, and Tamaulipas (Fig. 21). The record for "Gonzalez, Mexico; H. F. Wickham" might refer to a small town named Villa González Ortega in Zacatecas, approximately 100 km northeast of San Luis Potosí, where another specimen was collected by Wickham. Even if this is not the case, the presence of *V. bilineatus* would seem extremely likely in Zacatecas, as well as in extreme northeastern Jalisco.

Vaejovis bilineatus is a variable species in terms of color pattern and setal counts. In regard to the latter, it should be emphasized that although setal counts exhibit such great intraspecific variation that their taxonomic value is

Figure 21.—Map of northern and central Mexico depicting the distribution of *Vaejovis bilineatus*.

limited in this case, they are often more consistent in other groups of vaejovids. Most species of *Serradigitus* and the *Vaejovis mexicanus* and *nitidulus* groups, for example, have very consistent setation with only minor variation. Haradon's reliance on pedipalpal setal characteristics to delimit species and species groups in *Paruroctonus* indicates that they are relatively stable in that group as well.

Although variation in pedipalp chela dentition is usually minor, it is important to consider and quantify. It is recommended that, because atypical counts occasionally occur, the investigator check the dentitions of both the left and right chela fingers and examine as many specimens as possible. Variation in movable finger dentition in *Vaejovis spinigerus* (Wood) led Williams (1980) to misidentify specimens of this species from Isla Tiburon, Sonora as *V. gravicaudus* Williams (Sissom 1992). It should also be pointed out that, in some vaejovids, variation in chela dentition may be even less than seen in *V. bilineatus* or nonexistent—this was the case in previous studies on the *Vaejovis nitidulus* group (Sissom & Francke 1985; Sissom 1991).

The new information on color patterns in *V. bilineatus* presents a problem for those using older keys and descriptions to separate this taxon from *V. punctatus punctatus* Karsch. For example, in Hoffmann's (1931) key, the couplet separating the two forms is based entirely on whether specimens have two dorsal stripes or four. Studies on *V. punctatus* are in progress, and this species is also proving to be quite variable, especially in body size, coloration, and setation. Nevertheless, it is possible to distinguish *V. bilineatus* from *V. punctatus punctatus* as follows: in *V. punctatus punctatus*, (1) the internal face of pedipalp patella is flattened with a weak basal tubercle (not convex); (2) the dorsointernal and dorsoexternal carinae of the pedipalp patella are moderate and distinctly crenulated throughout (not weak and smooth to granular); (3) the pectinal tooth counts are usually higher, with male modal counts 18 and female modal counts 16; and (4) body size is distinctly greater with adult males approximately 30–40 mm long and females 40–50 mm. Additional differences will undoubtedly be found as the *V. punctatus* "complex" is revised.

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A NEW SPECIES OF *THERIDION* FROM NORTHEASTERN GEORGIA (ARANEAE, THERIDIIDAE)

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ABSTRACT. A new species of Theridiidae, ***Theridion ellicottense***, is described (from one adult male and one de-epigynated female) from the Blue Ridge Province of the southern Appalachian Mountains in northeastern Georgia.

The Family Theridiidae in North America is comprised of 27 genera and 232 described species (Roth 1993) and is relatively well known in terms of the ratio of described to undescribed species (Levi & Levi 1962). This is evidenced by the fact that within the largest genus, *Theridion* Walckenaer 1805, only three species have been described in North America north of Mexico since Levi's 1957 revision (see Gertsch & Reichert 1976; Levi 1980).

This new species is placed within the Theridiidae due to the presence of a tarsal comb and the lack of a colulus. Within the Theridiidae the generic placement of some species can be problematic (Levi & Levi 1962), particularly those species which comprise *Theridion* and *Thymoites* Keyserling 1884. Levi & Levi (1962) indicate that those species belonging to the genus *Theridion* have longer legs, are larger, lack a colulus, and lack the carapace modifications shown by male representatives of the species in the genus *Thymoites*. This new species has long legs (see Table 1), lacks a colulus and lacks carapace modifications. Therefore, we describe here a new species of *Theridion*, *Theridion ellicottense*, found in the southern Appalachians.

RELATIONSHIPS AND DIAGNOSIS

This new species appears to have affinities to those species which comprise both *Theridion* and *Thymoites*. However, features of the male carapace, pedipalp and chelicerae support our placement of this species in the genus *Theridion*. We must point out though, that independent of a *Theridion* species phylogeny, our hypothesis of the relationship of *Theridion ellicottense* to others in this genus is speculative. Levi (1957) constructs six species groups within *Theridion*. Based on features listed below, this species is placed in the *sexpunctatum* species group which is comprised of two species, *Theridion cheimatos* Gertsch & Archer 1842 and *Theridion sexpunctatum* Emerton, both known from the southern Appalachians (Levi 1957). Probable synapomorphies for this species group are: 1) the prominent conductor of the male pedipalp, 2) a subducted (hidden) embolus base, and 3) large elongate male chelicerae (Fig. 2). Males of *T. ellicottense* can be distinguished from males of *T. cheimatos* and *T. sexpunctatum* on the basis of features of the conductor (Figs. 3, 4). The conductor of the *T. ellicottense* palp is relatively thin and corkscrew shaped, whereas it is thick and linear in the other two species. As *T. cheimatos* and *T. sexpunctatum* share this feature of the male pedipalp, they may likely be sister species forming the series *ellicottense*—(*cheimatos*—*sexpunctatum*).

METHODS

All measurements were made with a dissecting microscope equipped with an ocular micrometer scale and are given in millimeters unless otherwise stated as a ratio. Whenever possible measurements were made at 50× and were accurate to 0.02 mm. Dorsal views of the spider were illustrated with the aid of a

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Table 1.—Measurements in mm of leg article lengths of male holotype (M) and female paratype (F), *Theridion ellicottense,* new species.

	Leg I		Leg II		Leg III		Leg IV		Pedipalp	
	M	F	M	F	M	F	M	F	M	F
Coxae	0.25	0.21	0.18	0.18	0.20	0.16	0.22	0.20	—	—
Trochanter	0.09	—	0.10	0.13	0.10	0.09	0.09	0.15	—	—
Femur	1.20	—	0.88	0.90	0.66	0.64	0.98	1.06	0.40	0.20
Patella	0.22	—	0.22	0.26	0.04	0.04	0.15	0.20	0.04	0.08
Tibia	1.20	—	0.72	0.64	0.52	0.40	0.82	0.80	0.18	0.14
Metatarsus	1.18	—	0.78	0.66	0.48	0.44	0.72	0.70	—	—
Tarsus	0.52	—	0.45	0.40	0.34	0.36	0.38	0.42	—	0.26
Total	4.66	—	3.33	3.17	2.34	2.37	3.49	3.40		

camera lucida. The male pedipalp was illustrated with the aid of a drawing grid.

Theridion ellicottense new species
(Figs. 1–4)

Types.—Male holotype and one female paratype were collected in a cove hardwood forest in Rabun County, Georgia (34°59′46″N, 83°06′54″W) at an elevation between 750–850 m (2 June [holotype] and 4 June [female] 1993; B. Dellinger). Types have been deposited in the U.S. National Museum of Natural History (Washington, DC) collection.

Etymology.—The specific name refers to the locality of collection of the type specimen, Ellicott Rock Wilderness Area. This area is named after the explorer and surveyor Andrew Ellicott (1754–1820) who, among other accomplishments, determined the border between North Carolina and Georgia in 1812.

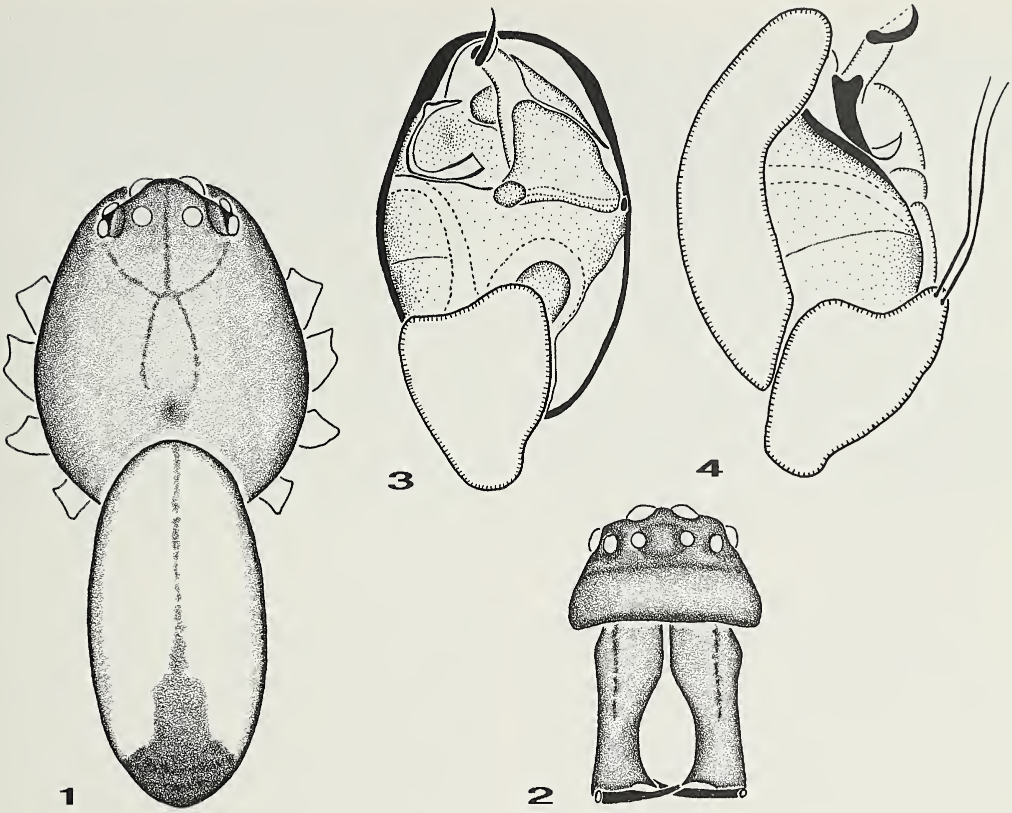
Male.—Total length 1.92 mm. Thoracic groove shallow depression. Cephalothorax 0.88 long, length 1.5 times width, dark green with tuning fork-shaped mark directly posterior to cephalic region. Cephalic region slightly raised, extends posteriorly half diameter of PME, anterior eye row slightly recurved, posterior eye row straight. Eyes roughly equal in diameter with AME slightly smaller. Eye diameters: PME 0.07; PLE 0.07; AME 0.05; ALE 0.06. PLE separated by 0.30. Remaining posterior eye row interdistances expressed as PME diameters: PLE-PME 1.0, PME-PME 0.7, PME-AME 0.5. ALE separated by 0.24 mm. Remaining anterior eye row interdistances expressed as ratios of AME diameter: ALE-AME 1.0, AME-AME 1.6.

Clypeus height three times AME diameter. Chelicerae 0.46 long, length 2.5 times width, light green with thin dark anterior-lateral stripe (Fig. 2). Cheliceral intermargin with oval opening, promargin provided with one large tooth (Fig. 2). Labium length 0.8 times width. Endite length 2.7 times width. Sternum 0.52 long, length 1.1 times width. Legs pale yellow without distinct markings. Leg formula I-IV-II-III. Coxae IV separated by 0.17.

Abdomen length 2× width. Dorsal surface of abdomen with dark posterior marking and thin dark line extending anteriorly (Fig. 1). No distinct lateral or ventral markings. (The illustration of the male is somewhat stylized. The actual type specimen's abdomen is wrinkled, possibly due to preservation).

Cymbium of male pedipalp length 1.8× width. Conductor distally located, with corkscrew shaped tip. Median apophysis mesally located and sickle-shaped. Thin short embolus with indistinct base (Fig. 3) tucks behind median apophysis. Patella of pedipalp with at least three macrosetae that extend to near tip of conductor. Two of these are visible and illustrated in the lateral view of the palp (Fig. 4).

Female.—Total length 2.12 mm. Thoracic groove less pronounced than in male. Cephalothorax 0.82 long, length 1.3× width, dark green without tuning fork mark. Cephalic region as in male. Posterior eye row recurved 0.5 times diameter of PME, anterior eye row slightly recurved. Eyes roughly equal in diameter with AME slightly smaller. Eye diameters: PME 0.08; PLE 0.06; AME 0.05; ALE 0.08. PLE separated by 0.26. Remaining posterior eye row interdistances expressed as ratios of PME diameter: PLE-PME 0.63; PME-PME 0.75; PME-AME 0.50.



Figures 1–4.—***Theridion ellicottense*** new species. 1, Male body, dorsal view; 2, Face and chelicerae of male; 3, Left male palp, ventral view; 4, Left male palp, lateral view.

Clypeus height 3× AME diameter. Chelicerae 0.30 long, length 2.1× width, lacking anterior lateral stripe of male. Labium length 0.8 times width. Endite length 2.5× width. Sternum 0.50 long, length 1.1× width. Legs as in male. Leg formula (leg I missing) IV-II-III (Table 1). Coxae IV separated by 0.20.

Abdomen length 1.2× width. Dorsum of abdomen like that of male with dark band extending anteriorly from spinnerets, thinning towards anterior ⅓ of abdomen. Epigynum was removed and misplaced by an outside party prior to description.

Natural History.—Specimens were obtained while using a modified version of a standardized collecting technique (Coddington et al. 1991). Therefore, specific microhabitat information is not known. The collection locality was located in a rich cove forest classified by the US Forest service as a white oak/northern red oak/hickory stand that originated around 1858. Site labels for the specimens indicate that the male was collected on the "ground" which includes all vegetation and/or structures at or below the knee level of the collector. Therefore, it is likely that the specimen was taken from low lying vegetation (most commonly consisting of *Leucothoe fontanesiana* [Highland Doghobble], *Castanea dentata*, *Lindera benzoin*, *Rubus canadensis*, *Hydrangea radiata*, *Carya glabra*, *Viburnum acerifolium*, *Ilex opaca*, and *Cornus florida*). The female's collecting label indicates that the specimen was taken "above ground". This includes vegetation and other structures from the knee level of the collector to as high as the collector can reach.

Distribution.—The species is known only from the type locality in the mountains of northeastern Georgia.

Other material examined.—None.

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OBSERVATIONS ON PREY CAPTURE AND ANTI-PREDATOR BEHAVIORS OF OGRE-FACED SPIDERS (*DEINOPIS*) IN SOUTHERN COSTA RICA (ARANEAE, DEINOPIDAE)

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ABSTRACT. Members of two apparently conspecific *Deinopis* populations from southern Costa Rica perform backward (aerial) strikes (in response to vocalizations and vibrating tuning forks) and forward strikes (to capture ambulatory prey). At daybreak these spiders quickly shift from foraging to cryptic behavior. This cryptic behavior, which is described and illustrated in detail, involves camouflage on a linear plant structure and/or stick mimicry. Body form, fringes of setae, palpal tarsus and claw shape, and color pattern all enhance the effectiveness of these cryptic behaviors.

The so-called ogre-faced or net-casting spiders of the genus *Deinopis* MacLeay 1839 are distinguished by remarkably large posterior median eyes and an unusual prey capture strategy. A small, highly extensible, cribellate capture web (a reduced orb-web) is constructed at nightfall, held at its four corners by the first two pairs of legs (Fig. 1), and actively manipulated to ensnare passing prey (Baum 1938; Roberts 1954; Theuer 1954; McKeown 1963; Robinson & Robinson 1971; Austin & Blest 1979; Gertsch 1979; Coddington 1986; Coddington & Sobrevila 1987; Penney & Whitehead 1995). Blest & Land (1977) have shown how the posterior median eyes, possibly the largest simple eyes of any land invertebrate, are specialized to concentrate light for nighttime visual detection of prey; and Blest (1978) has documented the spectacular and enigmatic diurnal cycle of rapid destruction (at daybreak) and synthesis (at nightfall) of the photoreceptor membrane in these eyes.

Coddington & Sobrevila (1987) showed that individuals of the Neotropical species *Deinopis spinosus* Marx 1889 can perform two quite different stereotyped attack behaviors, a backward strike to capture aerial prey and a forward strike to capture walking prey. In so doing, these authors resolved a controversy between Theuer (1954), who had described only backward strikes in *D. spinosus*, and Robinson & Robinson (1971), who observed forward strikes and were unable to elicit backward (aerial) strikes in their study of another species, *Deinopis longipes* F. O. P.-Cambridge, in Panama. Coddington & Sobrevila demonstrated that the backward strike is triggered by airborne vibrations, presented evidence consistent with Robinson & Robinson's conclusion that the forward strike is triggered by visual stimuli, and predicted that other *Deinopis* species would be found to exhibit both types of capture behavior.

Literature references to the cryptic behavior of *Deinopis* spiders during the daytime are brief, in part because these behaviors are so effective (Baum 1938; Theuer 1954; McKeown 1963; Robinson & Robinson 1971; Austin & Blest 1979; Gertsch 1979). Three such anti-predator postures have been observed (pressed flat against a branch, suspended head downward in midair with legs extended away from the longitudinal axis of the body in four tight pairs forming a cross, or hanging head downward in midair with legs I and II protracted and apposed in front and legs III and IV protracted and apposed behind the body to form a single linear "stick"), but no one has described the form of these anti-predator behaviors or associated structural design features in detail. Ackerman's (1926) description of twig/bud mimicry in *Menneus camelus* Pocock 1902 is, to our knowledge, the most detailed observation to date of a deinopid anti-predator tactic.

Our brief field study of the behavior of two Costa Rican *Deinopis* populations was designed to achieve two main objectives: 1) de-

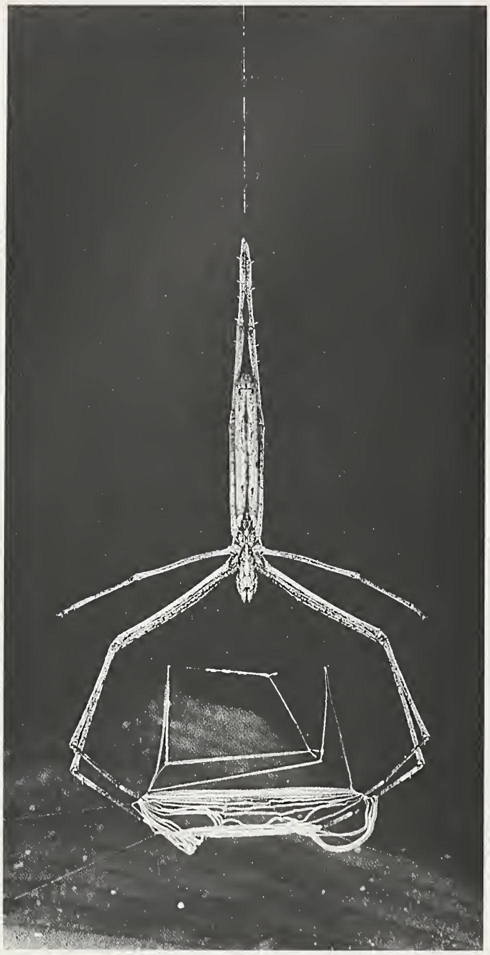


Figure 1.—*Deinopis* spider at Las Cruces in foraging posture above leaf surface.

termine whether these spiders perform backward strikes, and, if so, what stimuli trigger such strikes; and 2) describe in detail the diurnal anti-predator behavior of these spiders.

METHODS

We observed *Deinopis* from 5–12 March 1995 along trails in second growth forest at two locations in Puntarenas Province, Costa Rica: 1) the Las Cruces Field Station of the Organization for Tropical Studies near San Vito, and 2) above Rio Sierpe Lodge near the mouth of the Rio Sierpe on the Osa Peninsula. The nine spiders observed in this study, four from Las Cruces (spiders A, B, C, and D) and five from Rio Sierpe (spiders E, F, G, H, and I), were discovered at night in their prey capture posture (Fig. 1). Two (A and I) were penultimate males and the rest were probably penultimate females. Two were collected from each site and were examined by Brent Opell, who concluded that both populations probably represent the same undescribed species. These four specimens have been deposited in the Museum of Comparative Zoology.

When observing nocturnal behaviors, we used headlights with lenses covered by one (first night) or two (subsequent nights) layers of red cellophane. In order to determine whether this species performs the backward (aerial) attack, we tested six of the spiders with a tuning fork stimulus (256 Hz) after the method of Coddington & Sobrevila (1987). The tuning fork was positioned about 10 cm behind the capture-ready spider. A series of ten stimuli, five vibrating (experimental) and five not vibrating (control), were presented in alternating sequence to each spider with about 10 sec between successive stimuli. To observe the form and timing of the transition from nocturnal foraging behavior to diurnal cryptic behavior, we commenced observing a spider at about 0400 h, almost one hour before dawn. Still photographs were used to document cryptic postures.

PREY CAPTURE BEHAVIOR

The postures of capture-ready spiders and the form of the webs (Fig. 1) were virtually identical to those described by Robinson & Robinson (1971) for *D. longipes*. All capture-ready spiders were suspended above living or dead (lying on the ground) horizontal leaves. The capture web was held either parallel or perpendicular to the leaf surface, usually about 15–30 mm above it.

The first author's exclamation upon discovering the first spider triggered a backward (aerial) strike, and the short series of excited vocalizations that followed triggered three more such strikes in quick succession. Subsequent observations of other individuals confirmed that this species, like *D. spinosus* (Coddington & Sobrevila 1987) and two species of Australian deinopids (Austin & Blest 1979), responds consistently with backward strikes to hums and other vocalizations generated from a distance of up to 50 cm or more.

In the tuning fork stimulus trials (Table 1), 30 of the 40 presentations of a vibrating fork triggered strikes (all of which were backward strikes) and none of the 40 presentations of a

Table 1.—Results of tuning fork stimulus presentations to Costa Rican *Deinopis* spiders. See text for description of procedure.

Series #	Spider	No. of stimulus presentations: Vibrating	No. of stimulus presentations: Non-vibrating	No. of strikes: Vibrating	No. of strikes: Non-vibrating
1	A	5	5	5	0
2	A	5	5	5	0
3	C	5	5	4	0
4	D	5	5	5	0
5	E	10	10	6	0
6	H	5	5	3	0
7	I	5	5	2	0

non-vibrating fork triggered a strike. These results, in conjunction with the responses to vocalizations described above, show that airborne sounds and/or accompanying air currents are sufficient to stimulate the backward strike, and support the hypothesis that this mode of attack serves to capture flying insects. Like Coddington & Sobrevila (1987), we observed habituation (and/or fatigue) of this response; the first strike of a series was the most energetic strike (spiders A, D, and E each performed two strikes in response to the initial vibrating stimulus) and later strikes were less energetic than earlier ones in a given series (spiders E, H, and I failed to respond to the last 4, 2, and 3 presentations). Candidate sensory mechanisms which may permit *Deinopis* to detect these airborne vibrations include trichobothria and slit sensilla, both of which have been shown to play this role in other spiders (Barth 1982). Receptor ablation experiments could be used to test these hypotheses.

The aerial strike is very quick, and it is therefore difficult to observe and describe its mechanics without high speed movie or video cameras. In general, though, these strikes closely resembled the description and photos presented by Coddington & Sobrevila (1987). The spider's prosoma rotated backward, up, and away from the substrate as its snare was expanded by extension of legs I and II.

We observed two forward strikes like those described by Robinson & Robinson (1971) and Coddington & Sobrevila (1987), each in response to insect prey (a roach and a grasshopper) we encouraged to walk on the substrate below two different spiders. Both prey were wrapped but only the roach was eaten; the grasshopper was eventually released (rejected). Two spiders were observed feeding (in their foraging position) on prey items. Spider A was feeding on a 6–7 mm long beetle and spider E was feeding on a worker leaf cutter ant (*Atta*). The latter, and probably the former, would have been captured by forward strikes. We observed spider A use its pedipalps to bat at a small fly (about 2 mm long) that hovered and landed on the beetle; jerking movements of legs I and II also appeared to be responses to this probable kleptoparasite.

DIURNAL ANTI-PREDATOR BEHAVIOR

We observed spiders shifting from nocturnal to diurnal behavior 12 times over the course of our study. Spiders A–D were each observed doing this twice and spiders E, F, G, and I once each. We recorded the duration of this shift (from the onset of web takedown to completion of the cryptic posture) only five times (B = 3–4 min, E = less than 1 min, F = 28 sec, G = about 30 sec, I = 1.5–2 min), but recollect that none of the other seven observed shifts took more than 5 min except for the time that spider A was feeding on a beetle at the onset of dawn. Web takedown, which consisted of consolidating the capture web and at least some of the support elements, applying this package of silk to the mouthparts, and apparently digesting it, took from 20 sec–3 min. The spider then quickly climbed to its daytime resting spot by following a silk guideline and, with no more than a brief period of localized orientation and settling activity, assumed a cryptic posture. There was little variation in the time of day when this shift took place; the time when a spider assumed the cryptic posture ranged from 0455–0527 h (mean and SD = 0509 h ± 18) for the 11 instances when a spider was not feeding on prey. The single exception involved spider A, which moved to its daytime site at 0504 h but continued feeding in a partially cryptic posture well past daybreak and became fully cryptic at 0542 h, much later than its shift to a cryptic posture the following day (0455 h).

Perhaps the environmental cue which triggers this shift is the increase of light intensity to a particular threshold level or rate of increase at dawn; we were able to first detect

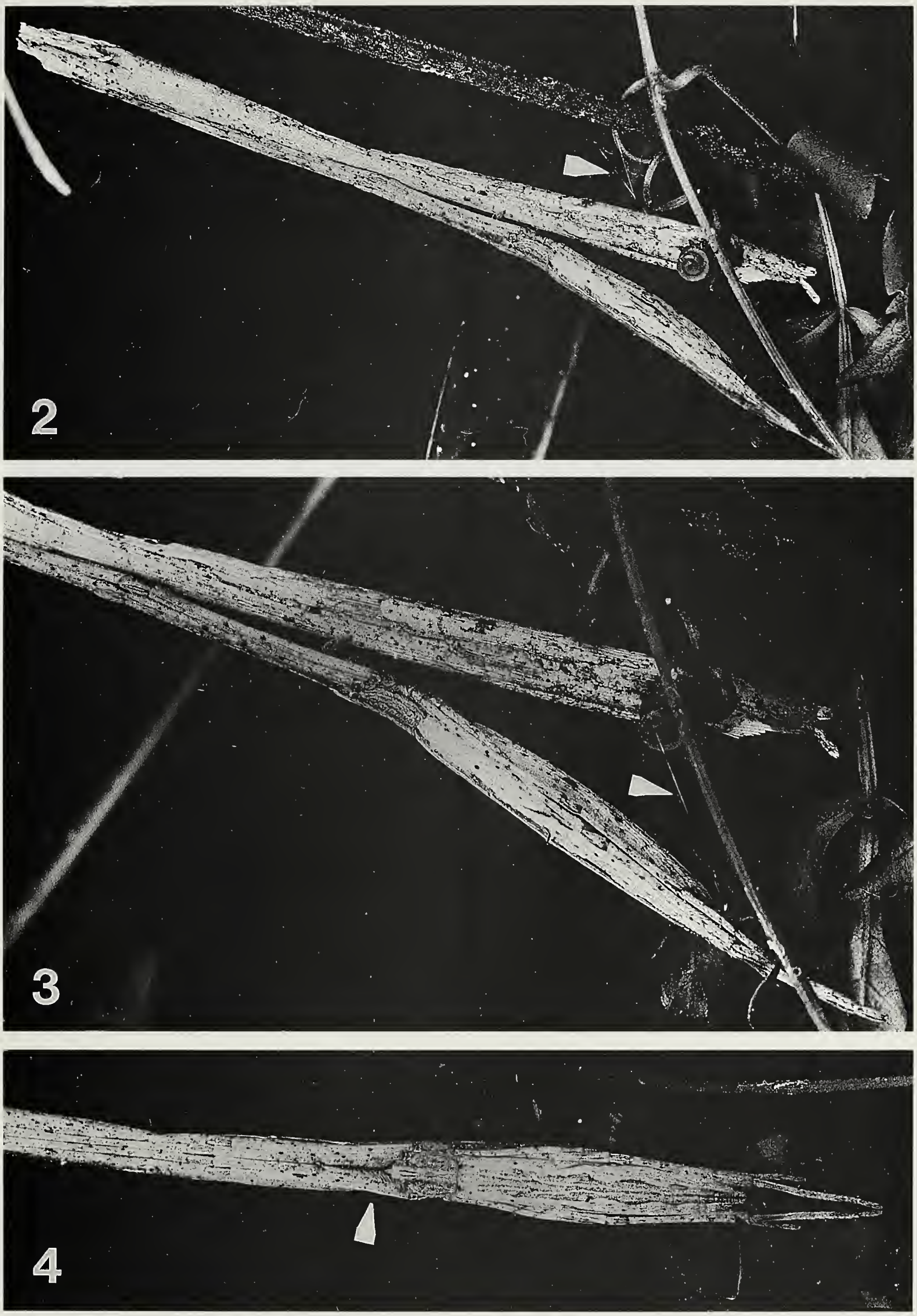
increasing light at about 0455 h each morning. It is also possible that the foraging-to-crypsis shift is a circadian rythym entrained by daylength. The only other potential cue perceived by us was the predictable and rather sudden onset of bird and howler monkey vocalizations at about 0515 h, but these events were too late to account for most of the observed shifts and no mechanism has been demonstrated in spiders for detecting such distant sounds.

Typically, as in *D. spinosus* (see Theuer 1954), the hiding site is close to the foraging site; the distance between these sites was recorded for five spiders and ranged from 25–80 cm (mean and SD = 58 ±21). Some site tenacity was observed during our short study. Spiders A, B, and C each foraged and hid in the same locations for the three nights and two days they were observed. Spider D likewise used the same foraging and hiding sites during the two days it was observed. Spiders E and G both moved to new but nearby sites during the second day of observation. Only spiders F and I moved so far that they were not found after the first day of observation. The presence of silk strands anchoring otherwise unattached pieces of vegetation which served as hiding substrates suggests that these spiders sometimes improve their hiding sites (Fig. 2).

Behavior, anatomy, and pigmentation all contribute to the remarkable diurnal crypsis of this spider. Assumption of the cryptic posture at dawn always involved attachment to a substrate, usually a linear plant structure (twig, vine stem, or petiole), typically a dead (brown) (Figs. 2–9), less often, a living (even green) one (Fig. 10). Most commonly the spider aligned its whole body and legs parallel to and against the substrate and appeared to become part of that substrate (Figs. 5–9), a strategy of camouflage or concealment (Robinson 1973, 1985). Less often, much or nearly all of the spider was positioned well away from the attachment substrate (Figs. 2–4, 10), and the spider mimicked a dead twig, relying on disguise rather than concealment (Robinson 1973, 1985). Attachment to the substrate was typically via silk (spinnerets to substrate) (Figs. 2–4) and usually by leg and/or palpal claws as well (Figs. 2-10). Most spiders were oriented head down (Figs. 5–11), but one was inclined in a slight head-up position (Figs. 2–4). Always legs I and II were protracted anteriorly and apposed and legs III and IV were protracted posteriorly and apposed along the sides of and beyond the tip of the abdomen so that the spider became a long slender sticklike unit (Figs. 2–11). Sometimes the spider "settled" into this posture with regular wavelike undulations of its legs and body; at other times the shift to this posture was more sudden and direct. While a given spider often hid at the same location for at least two consecutive days, it did not necessarily adopt the same posture on the same substrate (compare Figs. 2 and 3 to Fig. 10). This plasticity in the cryptic behavior of individual spiders is consistent with Robinson's (1985) suggestion that concealment is a "preadaptation to plant part mimicry." An individual which is positioned as in Figs. 2 and 3, so that part of its body is camouflaged on a stick and part is mimicking a stick, may illustrate an adaptive intermediate evolutionary step between pure concealment and pure stick mimicry.

Several anatomical design features contribute to camouflage and stick mimicry in this species: 1) The long slender body and legs produce a sticklike form, 2) the flat and posteriorly truncate carapace and anteriorly low and truncate abdomen lower the body profile and help conceal the transition from carapace to abdomen, and 3) the fringes of long setae proximally on the prolateral surface of the first femora and at the anterior median edge of the carapace fill and thus hide much of the gap between the femora (Figs. 4–6). 4) The tip of each palpal tarsus curves prolaterally and the palpal claws are long, features that help these claws grip and hold the body against cylindrical substrates (Figs. 2, 3, 7, 8). The spider's variegated light to dark brown pigment pattern closely resembles the coloration of many dead branches, vine stems, and petioles (Figs. 2, 3, 5–9).

When its body or its substrate is touched, a cryptic spider typically increases its crypsis by pressing its legs more tightly together and against the body, and, if positioned against a substrate, by flattening itself more tightly against that substrate (Figs. 5–8). Such a posture adjustment can effect a dramatic improvement in crypsis; sometimes it makes the spider temporarily disappear from view! When we tried to grasp one cryptic spider, it dropped several cm from the substrate and became sticklike while hanging free and motionless in midair from its dragline (Fig. 11).



Figures 2–4.—*Deinopis* spider C at Las Cruces; three views of spider in cryptic posture. Spider is attached by the claws of legs I and II, palpal claws, and dragline (see arrow in Figure 3) to undersurface of dead piece of stem or petiole which is suspended from a vine by silk (see arrow in Figure 2); 2, 3, Side view; 4, View from below (arrow points to gap between front femora, which is partly filled in by fringes of long setae on femora and caput).

Figures 5–8.—*Deinopis* spider E at Rio Sierpe; four views of spider facing downwards in cryptic posture on dead stem. 5, 6, Dorsal views; 5, Posture before stem is touched by observer; 6, Posture after stem is touched; 7, 8, Side views; 7, Posture before stem is touched by observer; 8, Posture after stem is touched. Arrows point to junction between prosoma and opisthosoma.

The defensive effectiveness of these behavioral and structural design features against visual predators is suggested by how much more difficult it is to find these spiders in daylight than at night. Despite careful searching, we were unable to find these spiders by day; this matches the experience of other authors with other deinopid spiders (Akerman 1926; Baum 1938; Robinson & Robinson 1971; Coddington & Sobrevila 1987; Penney & Whitehead 1995). On six occasions (three different spiders) we asked a person to locate one of our subject spiders during the daytime after defining a roughly 20 × 20 × 20 cm cubical search space containing the spider. None of the four people presented with this challenge succeeded. We suspect that the key selective agents responsible for the evolution and maintenance of this suite of cryptic defensive traits are to be found among diurnal insectivorous wasps, lizards, birds, and monkeys.

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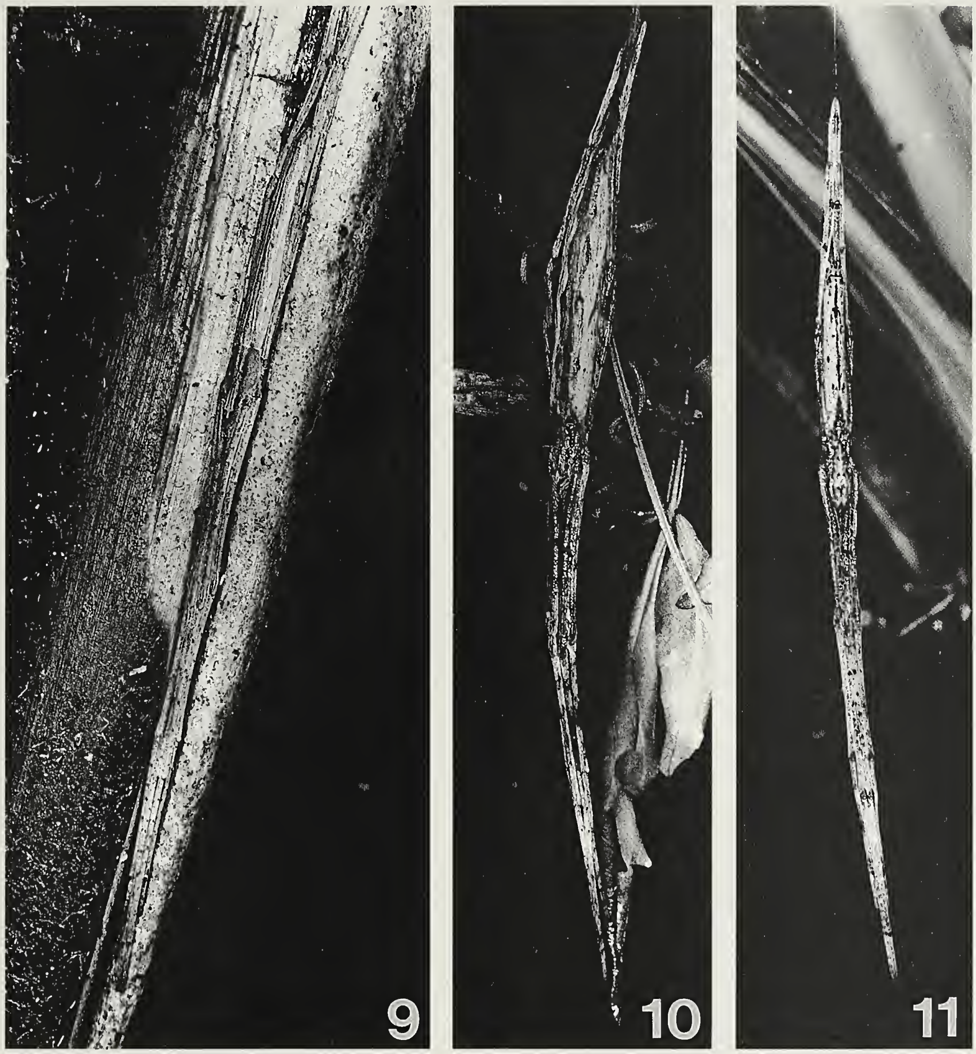

Figures 9–11.—*Deinopis* spiders at Las Cruces in cryptic postures; all facing downwards. 9, Spider R in longitudinal depression on stem; 10, Spider C hanging from slender vine and holding to leaf edge with anterior leg tarsi; 11, Spider D hanging motionless from dragline after being forced to drop from cryptic posture on plant.

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AN EXPERIMENTAL ANALYSIS OF INTRAGUILD PREDATION AMONG THREE GENERA OF WEB-BUILDING SPIDERS: *HYPOCHILUS*, *CORAS* AND *ACHAEARANEA* (ARANEAE: HYPOCHILIDAE, AMAUROBIIDAE AND THERIDIIDAE)

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ABSTRACT. We investigated predatory interactions among three species of web-building spiders which co-occur on sandstone outcrops along the Cumberland Plateau in east Tennessee: *Hypochilus thorelli* (Hypochilidae), *Achaearanea tepidariorum* (Theridiidae) and *Coras montanus* (Amaurobiidae). Previous studies have shown that these spiders are essentially ecological equivalents with respect to activity, website characteristics and prey capture and that each species preys on the others. This type of predatory interaction between potential competitors is referred to as intraguild predation. We performed removal experiments to determine the significance of intraguild predation for each of the species as predators and as prey. Three types of treatment plots were established: from each plot two of the three study species were removed (weekly, July-October 1993) and the third remained. Control plots were established from which no spiders were removed. We predicted that if the treatments resulted in removal of an important source of prey then: 1) the number of individuals of the remaining species should decline over time as a result of web-relocation, and 2) body condition of spiders remaining should be lower in the treatments than in the controls. If treatments had the effect of removing predation then the number of individuals remaining in treatment plots should increase relative to the controls where intraguild predation could occur. There were no significant differences in the number of spiders of the remaining species on treatment versus control plots, indicating that the treatment did not result in spider relocation as a response to potential food removal. However, at the end of the experiment body condition of *H. thorelli* was significantly lower on plots from which the other two species were removed than on control plots. This suggests that removal of the other two species may have resulted in removal of a significant source of prey for *H. thorelli*. In addition, we present evidence that treatments may have removed a source of predation on dispersing *A. tepidariorum* spiderlings.

Competition and predation are the two types of interspecific interaction thought to have major influence on community structure (Sih et al. 1985). Predatory interactions among members of the same guild (sympatric taxa that use similar resources, and thus may compete with each other: Root 1967; Polis et al. 1989; Simberloff & Dayan 1991) are termed intraguild predation (hereafter designated IGP). This type of predation is distinguished from predation in the traditional sense in that by eating a guild member, an individual not only gains energy and nutrients, but reduces potential competition for food. Intraguild predation has recently been proposed as an important and previously unrecognized factor which may influence the distribution, abundance and evolution of many species (Polis et al. 1989; Polis & Holt 1992).

Because most spiders are generalist predators on arthropods, different species may interact as both competitors and predators, making them ideal model organisms for the investigation of IGP. Several studies of IGP have included spiders; however, these studies found that spiders were intraguild prey of other taxa (Pacala & Roughgarden 1984; Polis & McCormick 1986, 1987; Spiller & Schoener 1988, 1990; Hurd & Eisenburg 1990; Moran & Hurd 1994). Studies of competitive interactions among spider species must consider the possibility of IGP. Riechert & Cady (1983)

tested for competition among four genera of web-building spiders inhabiting rock outcrops on the Cumberland Plateau in eastern Tennessee. They established experimental plots from which three of four species were removed and one species remained, and control plots from which no spiders were removed. Comparing population densities and egg production of spiders on experimental plots with those on controls, they found no evidence for competitive release by spiders remaining in the removal plots. However, on some of the removal plots they observed a negative effect of removals on the species remaining. Because they observed that almost 50% of the diet of one of the species studied consisted of spiders, they hypothesized that the absence of competitive release may have been due to the fact that they may have been removing prey rather than competitors (Riechert & Cady 1983; Wise 1993).

Though there is ample evidence that spiders prey on each other, (Polis 1981; Polis et al. 1989; Jackson 1992) to date no experimental studies have explicitly tested for IGP between spider species. Our study examined this possibility. We tested the hypothesis that IGP influences the distribution and abundance of three of the four species examined by Riechert & Cady (1983). We selected the Tennessee sandstone outcrop community as we felt it offered an especially promising model system to test for IGP: 1) there was already evidence that IGP might play a role in mediating competitive interactions (Riechert & Cady 1983), 2) because the three species all spin their webs on a vertical rock face we did not need to consider interspecific differences in microhabitat selection, and 3) the spiders are individually easy to observe and manipulate (e.g., compared to cryptic species or those in a more three-dimensional habitats such as vegetation). Our predictions were as follows: if the experimental treatments (removals) resulted in the removal of an important source of *food* for the species remaining on treatment plots, then 1) the number of individuals of the remaining species should decline over time and 2) body condition of the spiders remaining should be significantly lower in the treatment plots than in the control plots. The first prediction follows from the fact that when web-building spiders are deprived of food, they will relocate (i.e. move to a new web site, thus potentially leaving the plot). The second prediction is based on the fact that food-deprived spiders will have lower fat stores and thus lower body condition than well-fed spiders. If the experimental manipulations had the effect of removing *predators*, then the prediction was that the number of individuals of the focal species remaining in the treatment plots should increase relative to the control plots. This would be the case if the removals reduced the density of predators on the focal species.

METHODS

The study site was located along the sandstone outcrops of the Cumberland Plateau, in a canyon cut by Clear Creek where it is crossed by Lilly Bridge, in Morgan County, Tennessee. We studied the three most abundant species of web-building spiders: *Hypochilus thorelli* Marx 1888 (Hypochilidae), *Coras montanus* (Emerton 1889) (Amaurobiidae), and *Achaearanea tepidariorum* (C.L. Koch 1841) (Theridiidae). The lampshade spider, *Hypochilus thorelli*, is a cribellate spider whose distribution is restricted to rock outcrops in the Appalachian region (Forster et al. 1987). *Hypochilus* sits in the center of a tubular web which extends perpendicularly from the rock surface, pulled into a shape resembling a lampshade by support strands (Ferguson 1972). *Coras montanus* builds a funnel web, the base of which extends into crevices in the rock. *Achaearanea tepidariorum* builds a tangle web under ledges on the rock outcrop. Despite the differences in web structure, these three species are so similar in size, microhabitat, activity period, and prey captured that they have been termed "ecological equivalents" (Riechert & Cady 1983). The fourth species included in Riechert & Cady's study, *Araneus cavaticus* (Keyserling 1882) (Araneidae), was not included in this study because it was not common at our study site, and as an aerial web-builder shows less habitat overlap with the other three species (Riechert & Cady 1983).

Study plots were established along a continuous sandstone bluff running parallel to the east bank of Clear Creek approximately 1.2 km long and 18 m high. The specific section of rock used in the study was chosen for its relatively uniform structural features and be-

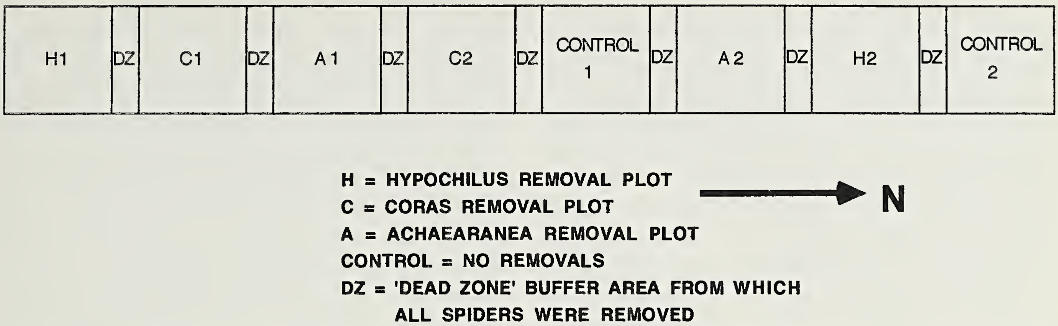

Figure 1.—Diagrammatic representation of study plots (not to scale). Treatment and control plots measured 20m long × 2m high. Plots labeled "H" are *H. thorelli* remaining plots (i.e., all other spider species were removed each week), plots labeled "C" are *C. montanus* remaining plots and plots labeled "A" are *A. tepidariorum* remaining plots. Plots labeled "DZ" are "dead zone" areas (measuring 1 m long × 2 m high) from which all spiders were removed on a weekly basis. Treatments were randomly assigned.

cause the entire length of this section faced the same compass direction (west).

Before beginning manipulations we quantified spider species present, the relative abundance of each, and the types of prey each captured. All spider species occupying our study cliffs were counted and assigned to one of three age categories: 1) spiderlings (recently emerged from egg sacs), 2) juveniles, and 3) penultimate to adults. Prey censuses were conducted weekly between 1 July–12 August 1993. The primary goal of the prey censuses was to quantify the extent of IGP by each of the three species. At each prey census all spiders on the study plots were visually examined in their webs and scored as to whether they were feeding or not. If they were eating we recorded the taxon of the prey (often prey was too badly macerated for identification). Prey censuses lasted approximately two hours, the length of time required to traverse the length of the study area and examine every web. To control for the effect of time of day on the taxa of prey captured, we scheduled censuses in a stratified fashion such that all two hour time intervals between 0600–2100 h were sampled once.

Removal experiments tested for the impact of IGP on each of the three species. Two replicates of each of three treatment (heterospecific removal) and control (no removal) plots were interspersed along a continuous 165.0 m length of rock outcrop according to a randomized design (Fig. 1). Each plot (treatment or control) was 20.0 m long × 2.0 m high, and was separated from adjacent plots by a 1.0 m long × 2.0 m high "dead-zone" from which all spiders were removed weekly. In treatment plots spiders of all species except one were removed. We designated each treatment plot by the name of the taxa *not* removed (i.e., *Hypochilus* remaining plots had heterospecifics removed weekly to examine the effect of heterospecific removal on *Hypochilus*). There were two replicates of each treatment: *H. thorelli* remaining plots, *C. montanus* remaining plots, and *A. tepidariorum* remaining plots. No spiders were removed from either control plot.

Spiders to be removed were counted and collected from treatment plots every seven days. The webs of removed spiders were scraped from the rock. The removed spiders were relocated 0.8 km to the end of the cliff and released. Initially all removed spiders were marked on the abdomen with enamel paint (Testor™, Testors Corp., Rockford, Illinois, USA) to determine if they could return to the study plots. However, after four weeks no marked spiders were found and marking was discontinued. Individuals of the focal species (designated to remain) were censused weekly. All spiders on the control plots were censused weekly, none were removed.

Spiders were censused weekly and recorded as belonging to one of two age classes: spiderlings or juveniles/adults. Spiderlings were the smallest size class present and were easily recognized as they were observed dispersing from egg sacs. Unlike our initial censusing, we did not distinguish between juveniles and adults as separate categories. Distinguishing

between juveniles and adults accurately required removing spiders for closer examination. This disturbance might have induced relocation which would have confounded our results. However, since the effects of heterospecific removal may be different for spiderlings than it is for other size classes we felt it important to at least distinguish between these two categories. For example, spiderlings dispersing from egg sacs may be more vulnerable to predation by larger juvenile and adult conspecifics and heterospecifics (Polis 1988).

Achaearanea tepidariorum is unique among the three focal species in that females lay their eggs in the web rather than elsewhere. During weekly censuses, the number of egg sacs per female *A. tepidariorum* was recorded. We also noted the condition of these egg sacs: unhatched, hatched with spiderlings in the mother's web, or empty. Using this information, we were able to estimate dispersal success by looking at the number of new spiderlings appearing on a plot each week as a function of how many egg sacs were observed hatching the previous week. Recently dispersed spiderlings are very small and easy to distinguish from individuals which have fed several times. The ratio of new spiderlings with webs to the number of recently hatched egg sacs the previous week gives us an index which allows us to estimate how successful dispersing spiderling are at establishing themselves in each plot.

The experimental study was initiated on 7 July and terminated on 16 October 1993. At the end of the experiment remaining spiders were collected from the plots and brought into the laboratory to be weighed and measured to assess nutritional condition. There was wide variation between plots in the number of *H. thorelli*. To reduce variation induced by varying sample size, we randomly selected 24 individuals (the number of spiders on the plot with the fewest individuals) from each of the heterospecific removal and control plots for weighing and measuring. Spiders were randomly selected using a modification of the wandering quadrat method (Catana 1955). Horizontal and vertical coordinates were established by laying a tape measure along the length of the plot and holding a measuring stick up against the plot. Sequential numbers selected from a random number table determined a horizontal/vertical point on the plot, and the *H. thorelli* nearest to this point was removed for measurement. The length of patella-tibia of leg 1 was measured to the nearest 0.01 mm using dial calipers. Spiders were weighed to the nearest 0.01 mg using an analytical balance. We used the residual index (Jakob et al. 1996) to compare the body condition of spiders on removal versus control plots. We regressed ln(body mass) on ln(length patella-tibia leg 1) of all spiders pooled (for each species) and used the residual distances of individual spider points from this regression line to serve as estimators of body condition (positive residuals indicate spiders fatter than predicted by the least-squares regression line, negative residuals indicate thinner spiders). We compared the residuals for spiders from the heterospecific removal plots to the control plots using a *t*-test.

Voucher specimens will be deposited in the collection of the Ohio Biological Survey, Museum of Biodiversity, Columbus, Ohio, USA.

RESULTS

Prior to our manipulations *C. montanus* was overall the most abundant species, represent-

Table 1.—Spider abundances on study plots before removals on 1 July 1993. Numbers in parentheses represent the percent of all spiders of a particular species on each plot (H1 and H2 = *Hypochilus* remaining plots, A1 and A2 = *Achaearanea* remaining plots, C1 and C2 = *Coras* remaining plots).

	Removal plots		
Species	H1	H2	A1
H. thorelli	30 (13.8)	45 (21.95)	29 (11.15)
A. tepidariorum	58 (26.6)	51 (24.9)	108 (41.54)
C. montanus	123 (56.4)	105 (51.2)	101 (38.85)
A. cavaticus	7 (3.2)	4 (1.9)	17 (6.54)
Pholcus sp.	0 (0)	0 (0)	5 (1.92)
Totals	218	205	260

ing almost 50% of spiders present (Table 1). *Achaearanea tepidariorum* ranked second in abundance, representing approximately 29% of spiders present, and *H. thorelli* was the third most abundant at approximately 14%. *Araneus cavaticus* and an unidentified pholcid were infrequent and variable in their occurrence on plots.

The percent of the total diet of each species represented by spider prey was substantial, ranging from 20–46% (Table 2). The diet of *C. montanus* was more difficult to quantify than the others as they often fed out of view (within their tubular retreat). This is reflected by the lower number of prey captures observed for this species (n = 17, Table 2). Including opiliones, over half of the diet of *H. thorelli* consisted of arachnids, with 46% represented by spiders alone. At least 10% of the diet of each species resulted from cannibalism or IGP. *Hypochilus thorelli* exhibited high predation on *C. montanus* (17% of total diet).

We were very effective at reducing heterospecific densities on the treatment plots. We suppressed the number of spiders targeted for removal by 65–90% (Table 3). We estimated our suppression of heterospecifics on the removal plots by taking the numbers seen on each plot prior to each weekly removal as a percent of the numbers of that species seen during the first census (Table 1). The weekly percents were averaged across the 12 week treatment period.

Despite the efficacy of removal of heterospecifics on removal plots, there was no significant response by the focal species. The number of the focal spider species left on each plot were not significantly different from the control plots. Because the initial number of focal spiders was variable, we examined the proportion of the initial number of the focal spider species at each census for statistical comparisons of treatments with controls. There were no significant differences between removal and control plots in the proportion of the initial number of juveniles and adults remaining for any of the three focal species (repeated-measures ANOVA on arcsin-square root transformed proportions: *H. thorelli* vs. controls: $P > 0.05$, $F = 0.178$, $df = 1$; *A. tepidariorum* vs. controls: $P > 0.05$, $F = 0.297$, $df = 1$; *C. montanus* vs. controls: $P > 0.05$, $F = 2.61$, $df = 1$). Visual inspection of the census data (Fig. 2) reveals no obvious trends. Thus the lack of significance is not likely due to a lack of power in these statistics resulting from the small sample size but rather a lack of an effect of heterospecific removal on focal species numbers.

There also appear to be no significant differences in the number of focal spiderlings establishing webs in heterospecific removal plots versus control plots as would have been predicted if removals reduced predation pres-

Table 2.—Percent of total observed prey captured by *Hypochilus thorelli* (n = 47), *Coras montanus*, (n = 17), and *Achaearanea tepidariorum* (n = 172). July to October along Clear Creek, Morgan County, Tennessee, USA.

	Predator		
Prey	*H. thorelli*	*C. montanus*	*A. tepidariorum*
H. thorelli	2	6	2
C. montanus	17	0	6
A. tepidariorum	4	6	0
Other spiders	23	12	14
Opiliones	17	6	13
Myriapods	0	12	6
Insects	37	58	59

Table 1.—Extended.

Removal plots			Controls	
A2	C1	C2	Control 1	Control 2
23 (7.9)	24 (10.57)	35 (16.2)	18 (5.22)	47 (24.3)
88 (30.2)	58 (25.55)	82 (37.96)	96 (27.83)	43 (22.3)
179 (61.5)	133 (58.59)	86 (39.8)	230 (66.66)	92 (47.67)
1 (0.04)	8 (3.52)	12 (5.55)	1 (0.30)	11 (5.67)
0 (0)	4 (1.76)	1 (0.50)	0 (0)	0 (0)
291	227	216	345	193

Table 3.—Mean reduction in heterospecific density from weekly removals. Numbers represent the number of individuals of each species present on each plot each week (before removal), expressed as a percent of the results of the first census, averaged over the 12 weeks of the experiment (mean percent ± SD). Plot designations are the same as used in Fig. 1.

	Species removed from plot		
Plot	*H. thorelli*	*C. montanus*	*A. tepidariorum*
H1	—	66 ± 13	65 ± 10
H2	—	65 ± 22	76 ± 11
C1	92 ± 8	—	84 ± 10
C2	83 ± 20	—	90 ± 5
A1	76 ± 25	72 ± 11	—
A2	81 ± 29	78 ± 11	—

sure on young spiders (repeated measures ANOVA on arcsin square-root transformed proportions; *H. thorelli* vs. controls: $P > 0.05$, $F = 0.671$, $df = 1$; *A. tepidariorum* vs. controls: $P > 0.05$, $F = 1.59$, $df = 1$; *C. montanus* vs. controls: $P > 0.05$, $F = 5.78$, $df = 1$; Fig. 3). However, comparing the index of spiderling dispersal (number of new spiderling webs in given week/number of hatching egg sacs in previous week) for *Achaearanea* plots versus control plots, we found that there were more new spiderlings settling in heterospecific removal plots than in control plots (repeated measures ANOVA on weekly index values; $P = 0.056$, $F = 16.29$, $df = 1$; Fig. 4).

There were no significant differences in the body condition of juvenile and adult *C. montanus* in heterospecific removal versus control plots at the end of the experiment (regression: $r^2 = 0.91$, $P < 0.001$; *t*-test on residuals: $t = -1.533$, $df = 33$, $P > 0.05$). There was a significant difference for *H. thorelli*, with individuals on control plots having higher residual values than individuals on heterospecific removal plots (regression: $r^2 = 0.76$, $P < 0.001$; *t*-test on residuals: $t = 2.9$, $df = 94$, $P < 0.05$; Fig. 5). This indicates that *H. thorelli* on control plots were better fed than *H. thorelli* on heterospecific removal plots. There were not enough juvenile or adult *A. tepidariorum* remaining at the end of the experiment to include in this analysis.

DISCUSSION

The removal of heterospecific guild members had no effect on the densities of focal web spider species in a cliff face web spider community. There was evidence, however, for improved settlement success for hatchling *A. tepidariorum* as a result of the removal of heterospecifics. We also present evidence for reduced foraging success of the species with the greatest predilection for araneophagy: *H. thorelli*. Thus, while elements of our study support the conclusions of Riechert & Cady (1983) that IGP interactions may have confounded the results of their competition experiment, we did not find strong support for IGP effects in this system.

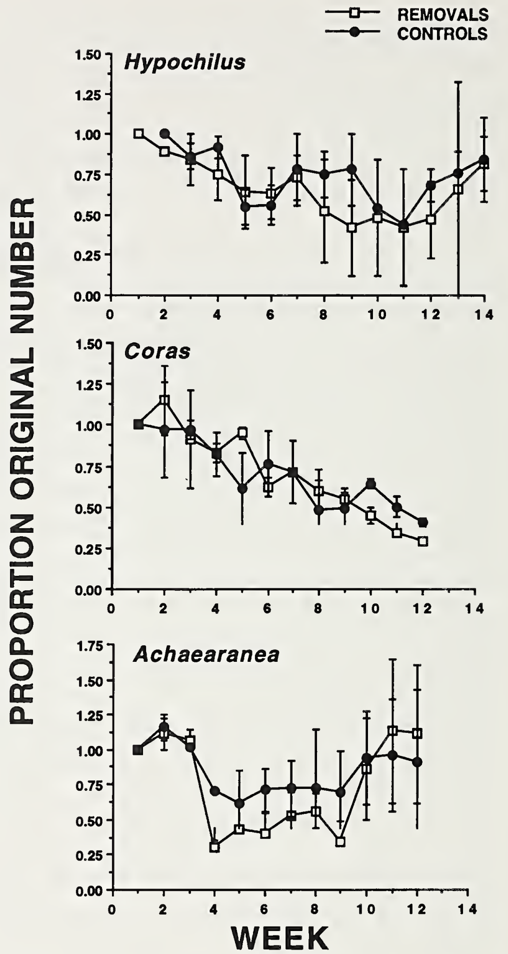

Figure 2.—Summary of the effect of heterospecific removal on focal spider species numbers. The proportions are the number of juvenile and adult spiders remaining on heterospecific removal (□) and control (●) plots during each weekly sampling interval divided by the numbers at the start of removals. Each point represents the mean of the two replicates, ± 1 SE.

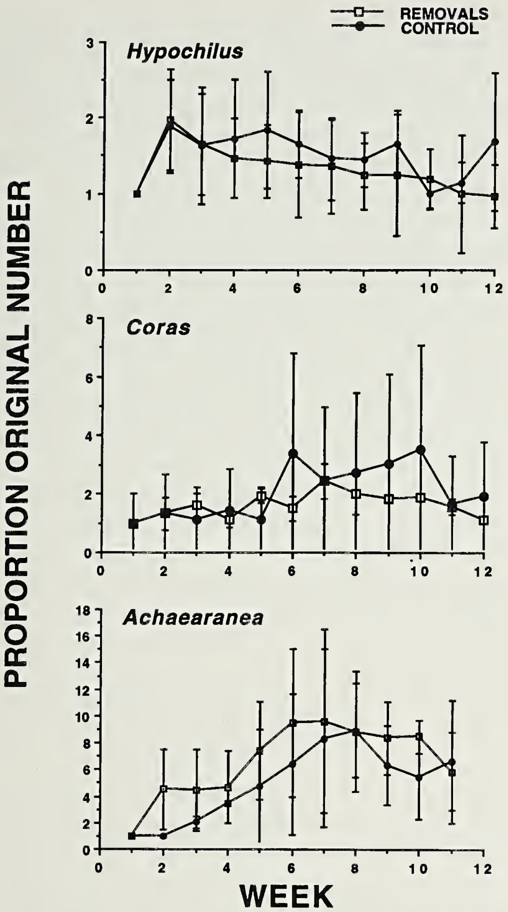

Figure 3.—The proportion of the initial number of spiderlings remaining on removal (□) and control (●) plots during each weekly sampling interval. Points represent the mean of the two replicates, ± 1 SE.

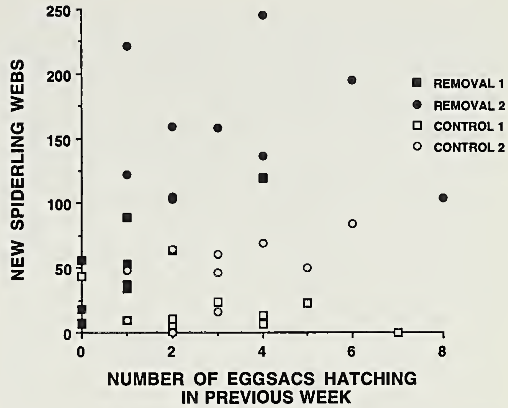

Figure 4.—The number of new *Achaearanea tepidariorum* spiderlings with independent webs on plots as a function of the number of hatching eggsacs on the plot in the previous week. Note that for any given number of eggsacs hatching, the number of new spiderling webs is generally lower in the control plots (open symbols) than in the removal plots (closed symbols).

Our prey census data are remarkably similar to those of Riechert & Cady (1983), especially the high proportion of the diet of *H. thorelli* composed of spiders (Table 2; Riechert & Cady: 47%; this study: 46%). Of the spiders included in the diet of *H. thorelli*, *C. montanus* makes up a large proportion (17%). This is perhaps not surprising given our finding that *C. montanus* is also the most common spider on the cliff face (almost 50%, Table 1). Therefore, if heterospecific removals result in a reduction in prey, we might predict to find the greatest impact of heterospecific removals on *H. thorelli* numbers remaining.

In order for removal experiments to effectively test for competition or predation, removals must reduce densities to a level that is less than weekly immigration back into plots. One of the problems encountered by Riechert & Cady (1983) was that high rates of immigration actually resulted in an increase in spider density in some plots, despite efforts to continually remove spiders (Wise 1993). In our study we were able to achieve a much greater level of success, with between 65–

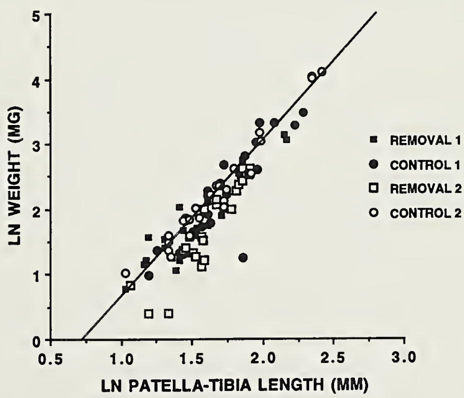

Figure 5.—Regression of ln(body mass) on ln(length of patella-tibia, leg 1) for *Hypochilus thorelli* collected from removal and control plots and the end of the study. Open symbols represent removal plots, closed symbols represent control plots. Note that most (71%) of the data points from removal plots fall below the regression line, in contrast to less than half (46%) of data points from control plots.

90% mean reduction in the original densities of spiders. Therefore, we believe that we were removing a significant portion of potential heterospecific competitors.

In our study we assumed that exploitative competition for prey was not an important interspecific interaction, after the results of Riechert & Cady (1983). However, since their experiment was not replicated this assumption may not have been valid (Wise 1993). If our removals resulted in a release from exploitative competition, we should have seen a higher residual condition index for spiders from heterospecific removal plots (i.e., evidence for better feeding history). However, there were no detectable differences in body condition of *C. montanus* on treatment versus control plots, and the body condition of *H. thorelli* was lower on the removal plots. While this supports our original hypothesis on the effects of removing intraguild prey from *H. thorelli*, it also allows us to infer that we were not reducing exploitative competition for non-intraguild prey (i.e., insects), supporting the conclusions of Riechert & Cady (1983).

There was some evidence to support the hypothesis that the removal of heterospecifics resulted in lower levels of predation on spiderlings on heterospecific removal plots versus control plots. While there were no differences in the numbers of spiderlings establishing webs in heterospecific removal and control plots during the course of the experiment, there may have been some differential success of *A. tepidariorum* spiderlings in the removal plots. Although there was an equal, or often greater number of hatching egg sacs in the control plots, our analysis indicates that there were relatively fewer spiderlings establishing webs in these plots a week after hatching (Fig.5). There are at least three potential explanations for this observation: 1) egg sacs hatching on control plots had fewer spiderlings as a result of lower fecundity or higher egg mortality, 2) less space was available for spiderlings to establish webs on control plots due to a greater overall density of webs, or 3) as spiderlings dispersed from their egg sacs they were intercepted and eaten by heterospecifics in the control plots. It would be difficult to observe such acts of predation in the prey censuses because *A. tepidariorum* spiderlings are so small as to become completely surrounded by the chelicerae of even a small heterospecific when being fed upon. Another possibility is that spiderlings avoid settling in areas with high densities of other web-builders. Such behavior could be adaptive in avoiding both predation and competition. Further experiments will be required to determine the mechanism to explain these results.

If removing heterospecifics from treatment plots resulted in removal of food, we predicted that the number of juvenile and adult spiders should decline in removal plots relative to control plots due to web relocation. No evidence was found to support this prediction for *C. montanus* or *A. tepidariorum*. We also predicted that a measure of body condition would show an effect of food limitation by the end of the experiment. No evidence was found to support this prediction for *C. montanus*. This would suggest that spiders make up a relatively insignificant proportion of the total prey biomass captured by *C. montanus*. This is supported by the results of our prey census (Table 2) in which we found that spiders make up 24% of prey observed by frequency. However, there was a significant difference in the body condition of *H. thorelli* in the direction predicted by the prey removal hypothesis. This result is consistent with the high proportion of spider prey in *H. thorelli*'s diet, and with the results of Riechert & Cady's (1983) study. Despite this evidence for removal of a significant amount of prey, we found no difference in the proportion of *H. thorelli* remaining on removal versus control plots, indicating that removal of food did not result in relocation by spiders. This may be due to the short time frame of the study. However, Vollrath (1985) similarly found that *Nephila clavipes* (Linne 1767) would leave prey-poor sites only under conditions of extreme prey deprivation. He suggests that high mortality while searching for new sites, or a low probability of finding a better site, might select for "acceptance" of prey poor conditions up to some threshold (Vollrath 1985).

While our study shows that other spider species form a significant part of the diet of *H. thorelli*, it is as yet unclear what benefits may be derived from the indirect component of intraguild predation, that is, removing potential competition for prey. All available evidence indicates that exploitative competition is not a factor in this spider community. Most experimental studies of web-building spiders

have found no evidence for exploitative competition (Schaefer 1978; Wise 1981; Horton & Wise 1983; Riechert & Cady 1983; this study), perhaps due to the fact that webs generally sample prey in a filtering fashion that rarely depletes local prey populations (Wise 1993). Though we did find evidence for significant predatory interactions in this rock-outcrop community, it may be that web-building spiders in general are poor candidates for investigating intraguild predation. Due to their sedentary nature, web-building spiders are unlikely to interact frequently unless they occur at very high densities (Wise 1993). Situations in which web-building spiders occur at high densities are usually restricted to conditions of abundant prey, which reduces the tendency for cannibalism or interspecific predation (Rypstra 1983, 1989; Dong & Polis 1992; Hodge & Uetz 1995). Interactions that result in predation may be rare for most species, restricted to chance interception of relocating individuals or aggressive, territorial encounters (Riechert 1982; Hoffmaster 1986).

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ESTIMATING SPIDER SPECIES RICHNESS IN A SOUTHERN APPALACHIAN COVE HARDWOOD FOREST

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ABSTRACT. Variation in species richness at the landscape scale is an important consideration in conservation planning and natural resource management. To assess the ability of rapid inventory techniques to estimate local species richness, three collectors sampled the spider fauna of a "wilderness" cove forest in the southern Appalachians for 133 person-hours during September and early October 1991 using four methods: aerial hand collecting, ground hand collecting, beating, and leaf litter extraction. Eighty-nine species in 64 genera and 19 families were found. To these data we applied various statistical techniques (lognormal, Poisson lognormal, Chao 1, Chao 2, jackknife, and species accumulation curve) to estimate the number of species present as adults at this site. Estimates clustered between roughly 100–130 species with an outlier (Poisson lognormal) at 182 species. We compare these estimates to those from Bolivian tropical forest sites sampled in much the same way but less intensively. We discuss the biases and errors such estimates may entail and their utility for inventory design. We also assess the effects of method, time of day and collector on the number of adults, number of species and taxonomic composition of the samples and discuss the nature and importance of such effects. Method, collector and method-time of day interaction significantly affected the numbers of adults and species per sample; and each of the four methods collected clearly different sets of species. Finally, we present recommendations to guide future research on the estimation of spider species richness.

Measures that describe or discriminate populations or communities, such as standing crop, basal area, population abundance, or species diversity indices, are useful tools for conservation, natural resource management, environmental monitoring, and land use planning (Magurran 1988). Many of these statistics, such as Shannon's diversity index or Fisher's log series, have been thoroughly tested by theoretical studies of their statistical behavior and accuracy and by use in many practical situations. It is a curious fact that similarly proven techniques to estimate species richness of conservation units or communities are lacking, given that the number of species is surely a fundamental, important and simple community parameter (May 1975, 1988, 1992; Pielou 1975; Palmer 1990; Bunge & Fitzpatrick 1993; Colwell & Coddington 1994; Gaston 1994; Samu & Lövei 1995). Quick, inexpensive and reliable methods for estimating the species richness of taxa at particular sites (alpha diversity) could provide useful input to conservation and land management decisions (Coddington et al. 1991). Although species richness is but one component of biological diversity and only one of many criteria conservationists and planners may use when evaluating sites (compare Vane-Wright et al. 1991; Williams et al. 1991; Faith 1992; Williams & Humphries 1994), it becomes especially important as the global loss of species by extinction accelerates and the need for species preservation increases. Regional or landscape diversity depends both on alpha (local) and beta (habitat) diversity; but because the latter measure also depends on estimates of alpha diversity that are repeated across the larger spatial scale at which beta diversity operates, the ability to estimate alpha diversity accurately assumes special importance. Estimating local richness for a defined place at a defined time is fundamental to estimates of biodiversity at larger spatial and temporal scales.

Our knowledge of the structure and pattern

of biodiversity at landscape scales is especially poor for those "megadiverse" groups such as terrestrial arthropods that are responsible for the vast majority of extant species diversity (May 1988, 1992; Stork 1988); yet it is at a landscape scale that conservation often operates, and at which faunas may actually be preserved or fragmented, as the case may be (Cornell & Lawton 1992). Various attributes and research initiatives point to the potential usefulness of spiders as indicators of arthropod species diversity in terrestrial communities. Spiders are a typical "megadiverse" group of substantial ecological importance. They are 1) among the most speciose orders of animals (Coddington & Levi 1991), 2) generalist predators which have an important collective impact on invertebrate herbivore populations (Riechert 1974; Riechert & Bishop 1990), 3) ubiquitous and easy to collect, and 4) nonspecialists can be quickly trained to make remarkably accurate counts of spider morphospecies (Oliver & Beattie 1993). Coddington et al. (1991) developed and field-tested a relatively simple protocol to sample and estimate the species richness (alpha diversity) of spiders in tropical forests.

This study assesses the usefulness of this protocol in estimating species richness in a temperate forest community by 1) examining the effects of method, time of day and collector on the number of individuals, number of species and species composition of the sample, and 2) comparing the richness estimates provided by different analytical approaches. Secondarily, we are interested in comparing the species richness of a site in one of the floristically richest regions of temperate North America (Whittaker 1972) with that of the tropical Bolivian sites sampled by Coddington et al. (1991). While the collecting methods used here were chosen for their efficiency in sampling spiders, we hope the overall approach, and especially the analytical methods, can be generalized to other diverse taxa. The fundamental rule is to choose sampling methods according to the natural history of the taxon without sacrificing heuristic measures of sampling effort.

METHODS

Study site.—The study site is a southern Appalachian cove hardwood forest at 750–850 m elevation, located in the Ellicott Rock Wilderness Area in Rabun County, Georgia (34°59′N, 83°06′W). The US Forest Service classified this site as a mature white oak/northern red oak/hickory timber stand originating in about 1858. Winter aerial photos reveal that white pine trees are more common here than in most southern Appalachian hardwood coves. Schafale & Weakely (1990) classify this site as a rich cove forest with a transition into montane oak-hickory forest. The site contains one of 57 permanent vegetative diversity plots established in 1990–1991 for monitoring habitat change in the Ellicott Rock Wilderness Area (Patterson 1994).

Data collection.—Four collection methods were chosen to access the most diverse components of the spider fauna: aerial hand collection, ground hand collection, beating and Tullgren funnel litter extraction. We used time as a measure of sampling effort to make the first three methods comparable. One sample unit equalled one hour of uninterrupted time during which all putatively adult spiders were collected into 80% ethanol. A 1 h sample unit yielded a statistically tractable number of individuals per sample and allowed for a sufficient number of replicate samples to conduct statistical analyses. Day (900–1800 h) and night (2000–0300 h) samples were collected in order to access both diurnal and nocturnal species. Each collector was limited to five or fewer sample hours for each day or night collection period. Total sampling intensity was dictated by the number of adult spiders required for richness estimation. Coddington et al. (1991) guessed that roughly ten times as many specimens as species in diverse tropical communities might yield sufficiently accurate estimates of species richness. Since Coyle's (1981) study suggested that 60–120 species were accessible in a mature pine-hardwood forest within 5 km of our site, and since preliminary sampling (2 September 1991) at our site averaged 12 adult spiders per hour, we judged that 100 sampling hours would be adequate.

The three time-based collection methods involved capturing spiders by hand and with an aspirator. The aerial and ground hand collection methods are synonymous with the "looking up" and "looking down" methods, respectively, of Coddington et al. (1991). Aerial sampling required searching vegetation from knee height up to maximum arm's reach overhead. Ground collection required searching on

hands and knees, exploring the leaf litter, logs, rocks and plant surfaces that were below knee level. Beating entailed striking vegetation with a stick, catching the falling organisms on a 0.5 m^2 canvas sheet held horizontally below the vegetation, and aspirating and picking the spiders off the sheet. The number of such beating/collecting events averaged 22 per one hour sample. Two of the three collectors in this study were experienced collectors with moderate practice at identifying southern Appalachian spiders; the third had no prior experience collecting or identifying spiders.

Plotless areas (*ca.* 500 m^2) that allowed for adequate sampling opportunities and precluded collection interference were roughly delimited in the field. The collectors, each using a different method, operated simultaneously in each such area for one hour. Flagged boundaries prevented resampling on subsequent visits. In order to restrict collecting to a fairly homogeneous vegetative type, distinctly different habitats, such as ridge tops, steep rock outcrops, and *Rhododendron* thickets were avoided. Approximately 2.5 ha were sampled.

Leaf litter was removed by hand from a 2 m^2 area and placed in a plastic bag. In the laboratory this litter was placed in 50–60 cm diameter Tullgren funnels with 60 W light bulbs and 6–8 mm mesh screens, and spiders were extracted into alcohol until the litter was dry or nearly so. Data from the 11 litter samples were included in richness estimates but omitted from time-based comparisons.

Sampling dates and number of one hour samples (n = 122) were as follows: 2 September 1991 (n = 2); 6–9 September (n = 50); 13–15 September (n = 35); 22 September (n = 18); and 5–6 October (n = 17). The October collection was added primarily to see if species represented by penultimate instars in the September collections would mature before winter. Collectors were assigned methods so that analysis of variance cells were equably represented; no more than two replicates of any one collector/method combination occurred in any single 5 h collecting period. Each of the 11 litter samples was treated as equivalent to 1 h of collector effort for the purposes of richness estimation. Total sample number for estimation was thus 133.

This protocol differed from that used by Coddington et al. (1991) by using time as a measure for beating, adding Tullgren-funnel extraction of area-based litter samples, extending sampling to as many as 10 h (rather than only 5) in a 24 h period, avoiding resampling of areas, and in accessing a larger area (2.5 ha) rather than confining collectors to one hectare.

Only adult spiders were identified, counted and used in the analyses because identifying juveniles to species level is difficult, time consuming and fundamentally ambiguous in many cases. Voucher specimens for each species identified in this study and a portion of the duplicates have been deposited in the Smithsonian Institution (USNM).

Statistical analysis.—Richness estimates were obtained using six different approaches that differ in theoretical assumptions and the kind of data required. The classic continuous lognormal distribution (Preston 1948; Magurran 1988; Ludwig & Reynolds 1988; Colwell & Coddington 1994) is a parametric technique requiring relative abundance data. We also fitted the Poisson lognormal (Bulmer 1974) because its assumptions are better suited to discrete data than are those of the continuous lognormal. We tested the fit of both lognormal models to the data with Chi square statistics. The estimator proposed by Chao (1984), hereafter "Chao 1," is non-parametric, but also requires relative abundance data. The remaining three techniques are non-parametric but require only presence-absence data: the "Chao 2" estimator (Chao 1987), the jackknife (Heltshe & Forrester 1983), and species accumulation curves fitted to a rectangular hyperbola (the "Michaelis-Menten equation") (Lamas et al. 1991). We programmed SYSTAT (Version 5.02) routines to calculate all richness estimates except the Poisson lognormal, for which we used Ross (1987). We also used EstiMateS 3.1 (R. K. Colwell unpubl.) to investigate the behavior of estimators under randomized sample orders (see below). Where possible we provide variance estimates for the richness estimates. Point estimates of species richness are most valuable when combined with measures of variability because the reliability or precision of the estimates is conveyed as well.

We followed Magurran (1988) in fitting the lognormal model (Preston 1948) to the data. Octaves falling to the left of the zero octave represent species that could have been collected if more sampling had been done, while

octaves to the right represent actual sampling results. The null hypothesis that relative abundances are lognormally distributed is assessed by a Chi square statistic (df = number of octaves − 3). The area under the normal curve estimates the number of species in the universe being sampled. There is no analytic formula for the variance of the area under the curve (Pielou 1975), so measures of variability are not available for the lognormal estimate.

Chao (1984) proposed the following nonparametric estimator (Chao 1, Colwell & Coddington 1994) for species richness (S^*):

$$S_1^* = S_{obs} + (a^2/2b) \tag{1}$$

where S_{obs} is the number of species observed, a is the number of singletons, and b is the number of doubletons. Chao originally used a bootstrapping procedure to calculate a variance, but later work suggests the same algebraic formula for the variance of the Chao 2 estimator (see below) may serve for Chao 1 (Chao 1984, 1987, pers. comm.). Note that the Chao 1 estimator reaches its maximum of about one-half the square of the observed richness when all species save one are singletons and considers the inventory complete when all species are represented by at least two individuals.

The Chao 2 estimator (Chao 1987; Colwell & Coddington 1994) originally dealt with the estimation of population size when the capture probabilities of individuals vary. This is formally equivalent to estimating the richness of a community when the abundance of species vary, and therefore her technique may also be used to estimate species richness. Chao 2 requires replicated samples (unlike Chao 1) and takes the same algebraic form as the Chao 1 estimator, above. Thus,

$$S_2^* = S_{obs} + (L^2/2M), \tag{2}$$

where L is the number of species found in only one sample ("uniques", regardless of abundance in those samples), and M is the number of species found in just two samples ("dupes", regardless of their abundance). The variance is

$$\mathrm{var} = M\left[\left(\frac{L/M}{4}\right)^4 + (L/M)^3 + \left(\frac{L/M}{2}\right)^2\right]. \tag{3}$$

The formula for var (S_1^*) is the same, but with a replacing L and b replacing M. Note that Chao 2 reaches its maximum of about one-half the square of the observed richness when all species save one are uniques, and, conversely, considers the inventory "complete" when all species occur in at least two samples.

The non-parametric jackknife estimator proposed by Heltshe & Forrester (1983) is

$$S_3^* = S_{obs} + L\left(\frac{n-1}{n}\right), \tag{4}$$

where n is the number of samples. The variance is

$$\mathrm{var}(S_3^*) = \frac{n-1}{n}\left(\sum_0^{S_{obs}} j^2 f_j - \frac{L^2}{n}\right), \tag{5}$$

where f_j is the number of samples with j of the L unique species. The jackknife reaches its maximum of $\approx 2S_{obs}$ when all species are uniques and considers an inventory complete when all species are known from at least two samples.

Species accumulation curves are a classic, but informal way to assess the completeness of an inventory (Pielou 1975; Soberón & Llorente 1993). As individuals of a population are sampled, new species are encountered rapidly at first, but subsequently appear less frequently as the asymptote of species accumulation is approached (Miller & Wiegert 1989). An equation for a two parameter hyperbola, popularly known as the Michaelis-Menten equation, has been used to estimate the asymptotes of such curves, simply because it fits many data sets reasonably well (e.g., Lamas et al. 1991). It is

$$S_4^* = S_{obs}(n)\left(\frac{B+n}{n}\right), \tag{6}$$

where S_4^* is the estimate of the asymptote (the species richness) and B is a fitted constant (actually the number of samples needed to collect half the total species). As noted by Raaijmakers (1987) and Colwell & Coddington (1994), most efforts to calculate a variance for this estimator (e.g., by least squares or regression) are flawed by assuming independence among data points. However, one can at least calculate S_4^* for a large number of randomized accumulation orders and calculate the variance of this sample of estimates (Colwell & Coddington 1994). This statistic measures the variability in the data due to sample composition and richness. Richer samples added earlier

Table 1.—Summary values and richness estimates for the Ellicott Rock samples. Sampling intensity is ratio of number of adults to observed species richness. See "Methods" section for explanation of bounds on estimates.

	Sample sets			
	A (Samples collected Sept. 2–13)	B (Samples collected Sept. 14–Oct. 6)	C (All except Oct. samples)	D (All samples)
Summary values				
No. of samples	64	69	114	133
No. of adults	751	878	1452	1629
Observed richness	67	74	85	89
No. of singletons	25	24	25	26
Sampling intensity	11.2	11.9	17.1	18.3
Estimators				
Poisson lognormal	207 ± 315	157 ± 127	179 ± 156	182 ± 126
Chao2	101 ± 35	135 ± 69	131 ± 49	128 ± 40
Chao1	102 ± 37	110 ± 40	124 ± 43	123 ± 35
Jackknife	93 ± 10	101 ± 12	111 ± 11	117 ± 11
Lognormal	98	92	106	114
Michaelis-Menten	89 ± 14	87 ± 18	100 ± 12	104 ± 13

tend to cause a more pronounced shoulder and earlier asymptote. We performed 100 such randomizations and calculated informal bounds on the estimate (2 SD) of the resulting 100 asymptote values.

Finally, to gauge the adequacy of the inventory for estimating richness, we again computed 100 replicate accumulation curves by randomized sample order, and, after the addition of each sample, calculated three estimators (Chao 1, Chao 2, and jackknife), which Colwell & Coddington (1994) found to be especially effective. Means of observed species accumulation and each estimator were plotted against sample number. This analysis reveals the behavior of the richness estimators as information accumulates (the empirical species accumulation curve). A good estimator should reach a stable asymptote long before the empirical curve (i.e., given few data). If the richness estimators do reach a stable plateau, even if the observed curve is still rising by the last sample, the inventory may be adequate to estimate richness of the fauna (Colwell & Coddington 1994). Conversely, if the estimators are still climbing by the end of the inventory, richness estimates may still be subject to undersampling bias.

Effect of sampling methods on results.—Analyses of variance were used to identify significant differences ($P < 0.05$) among the treatment variables (collector, method and time of day) in both number of adults and number of species collected, and Tukey HSD tests were used in determining pairwise significant differences (at $P < 0.05$). Descriptive statistics, ANOVAs, and Tukey tests were calculated using SYSTAT. The Bray-Curtis (1957) index of similarity,

$$C = \frac{2w}{(x + y)} \tag{7}$$

where x is the total number of adults collected by one method, y is the total number of adults collected by the other method, and w is the sum of the lesser values for those species present in both samples, was used to assess the effect of collection method on the taxonomic composition of samples.

RESULTS

A total of 6666 spiders was collected in the 133 samples, including 1629 adults representing 19 families, 64 genera, and 89 species (see Appendix). We define "sample intensity" to be the ratio of individuals (adults) to species, here 18.3:1. We define "inventory completeness" to be the percentage of species represented by singletons, here 29% (Table 1). While inventory completeness rarely goes to zero, in well-sampled faunas it is likely to be low, whereas in sparse samples from rich

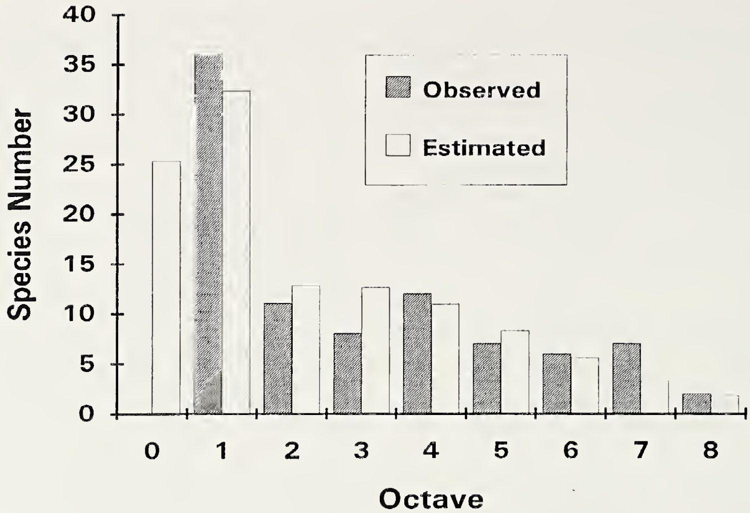

Figure 1.—Fit of the data of Appendix ("observed") to the continuous lognormal distribution (estimated). $X^2 = 6.8$; $df = 6$; $0.5 > P > 0.1$. The distribution is truncated on the left.

communities it is likely to be high. The collected data conformed to an expected skewed frequency distribution (Williams 1964), with many species represented by few individuals and few species by many individuals. Only three species had abundances greater than 100, the most abundant being 186.

Richness estimates.—For the complete data set, the richness estimates derived from all estimators except the Poisson lognormal agreed fairly closely and their confidence intervals overlapped (Table 1). In general, estimates derived from approximate halves of the data (subsets A and B) were lower than those based on nearly all (subset C) or all (set D) of the samples. For all these sample sets but set A, the rank order (from low to high) of estimators was Michaelis-Menten, lognormal, jackknife, Chao 1, Chao 2, and Poisson lognormal.

The truncated species abundance distribution for the complete data set spans eight octaves (Fig. 1). The frequency distribution was slightly bimodal, but the continuous lognormal model fit reasonably well ($0.1 < P < 0.5$). Acceptable fits were also obtained for all four partitions of the data, as judged by a Chi square goodness of fit test.

The species accumulation curve (Fig. 2) reveals that new species were still being added when sampling stopped and that the asymptote had not been reached, despite the relatively high sample intensity. Likewise, curves representing the mean values of the Chao 1, Chao 2, and jackknife estimators at each sample increment for 100 randomizations of sample sequence have not reached asymptotes (Fig. 3).

Effects of method, time of day and collector.—Table 2 summarizes the data in the Appendix on numbers of adults and species collected by method and time of day. The number of adults collected per sample was highly variable for all methods but especially so for the litter samples. Three-way ANOVA's of the 122 time-based samples (litter samples omitted) showed that method and collector, but not time of day, significantly affected both the number of adults and species per sample and that the method-time of day interaction significantly affected both the number of adults and species per sample. Tukey tests showed that aerial and ground collecting yielded significantly more adults per sample than beating, and significantly more species than litter sampling.

The Bray-Curtis similarity indices are low for all pairwise comparisons of the samples of each of the four collection methods (Table 3). Even samples collected with the most similar methods (aerial and beating; ground and litter), were quite distinct taxonomically. Of the 57 species collected by aerial and/or beating methods, 17 (30%) were unique to aerial collections and 13 (23%) were unique to beating. Of the 59 species collected by ground search-

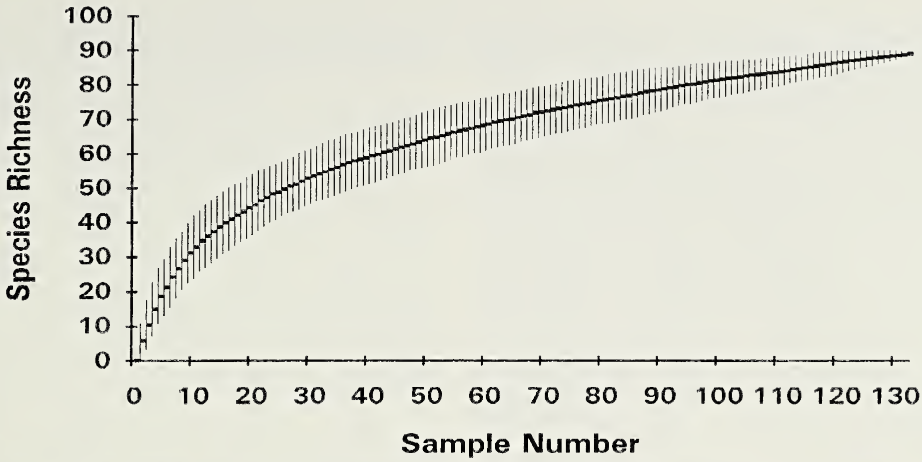

Figure 2.—The empirical species accumulation curve for the data of Appendix. Samples were accumulated randomly 100 times, and the mean ± two standard deviations plotted.

ing and/or litter extraction, 37 (63%) were unique to ground samples and 6 (10%) were unique to litter. Of the total 89 species observed, 12 species were caught only by aerial collecting, 15 only by ground collecting, 8 only by beating, and 5 only by litter extraction. Of these 40 species, 26 (65%) were singletons. Day and night samples for a given method have much higher indices of similarity than do samples collected by different methods (Table 3), indicating that contrasts between methods are much stronger than contrasts between day and night. Nevertheless, 14 species (16% of the total) were collected only at night and 18 species (20% of the total) were collected only during the day.

Tukey tests attributed the significant effect of collector on both the mean number of adults and species to the difference between collectors 1 and 2 (the most *versus* the least

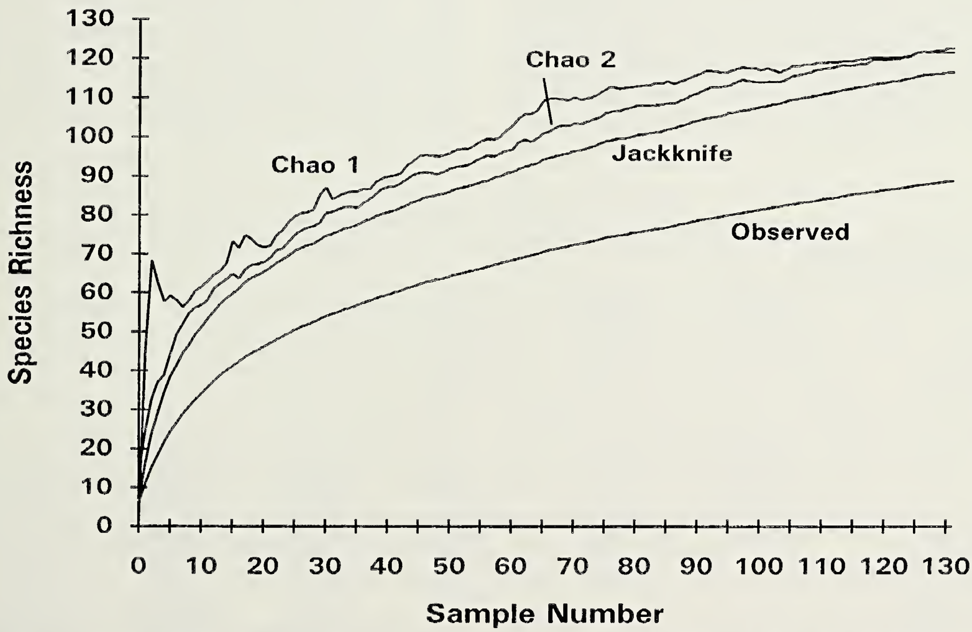

Figure 3.—Mean values of observed species richness and Chao 1, Chao 2, and jackknife estimators at each sample increment for 100 random orders of sample addition.

Table 2.—Summary of numbers of adults and species by collection method and time of day. Standard deviations of the mean number of adults and species per sample are given for method subtotals and for totals. n = number of samples.

	n	No. of adults	Mean no. of adults per sample	% of total adults	No. of species	Mean no. of species per sample	% of total species
Aerial							
Day	21	322	15.3	20	28	6.0	31
Night	21	315	15.0	19	33	6.5	37
Subtotal	42	637	15.2 ± 7.8	39	44	6.2 ± 2.1	49
Ground							
Day	20	222	11.0	13	41	6.1	46
Night	20	351	17.6	22	34	6.7	38
Subtotal	40	573	14.3 ± 6.7	35	53	6.4 ± 2.4	60
Beating							
Day	20	195	9.8	12	30	5.0	34
Night	20	113	5.7	7	26	3.8	29
Subtotal	40	308	7.7 ± 4.5	19	39	4.3 ± 2.0	44
Litter	11	111	10.1 ± 14.9	7	22	3.8 ± 3.4	25
Total	133	1629	12.2 ± 8.1	100	89	5.5 ± 2.5	100

experienced and productive collectors, respectively). Each collector's performance (measured by average number of adults/sample) varied considerably during the study (Table 4). A two-way ANOVA of the effects of date and collector indicated a significant effect of collector on the number of adults collected, due to the difference between collectors 1 and 2 during the first sampling period. After this first period, there were no significant productivity differences among the collectors. Although not significant, the average number of adults collected per sample did decrease slightly during the final sampling period (Table 4).

DISCUSSION

These methods estimate only the portion of the total Ellicott Rock spider fauna present as adults in the area we sampled, during the time we sampled, and accessible to the methods we used. These are, therefore, estimates of the "instantaneous" species richness of the ground and understory strata of that forest site. They certainly underestimate the true species richness, meaning all those species

Table 3.—Bray-Curtis similarity indices.

A. Collecting methods

	Ground	Beating	Litter
Aerial	0.091	0.261	0.003
Ground		0.066	0.175
Beating			0.029

B. Method and time of day combination

	Aerial night	Ground day	Ground night	Beating day	Beating night	Litter (day)
Aerial day	0.575	0.088	0.048	0.116	0.128	0.005
Aerial night		0.086	0.084	0.180	0.257	0.005
Ground day			0.496	0.077	0.167	0.144
Ground night				0.059	0.082	0.147
Beating day					0.494	0.163
Beating night						0.045

Table 4.—Mean number of adults collected per sample by collector and sampling period. Number of sample hours in parentheses.

	Sampling period			
	1 (Sept. 6–9)	2 (Sept. 13–15)	3 (Sept. 22)	4 (Oct. 5–6)
Collector				
1	14.8 (20)	15.5 (14)	21.0 (4)	10.6 (5)
2	9.0 (20)	12.5 (14)	9.0 (9)	6.0 (6)
3	13.0 (10)	11.6 (7)	16.4 (5)	12.0 (6)

that successfully bred at that site during the annual cycle in which we sampled. Even given this definition of the "local" fauna, species may go locally extinct or immigrate from one year to the next, to say nothing of showing great variation in abundance (Wolda 1978). "Local species richness" necessarily varies with the time scale on which it is defined. These estimates are snapshots—they should underestimate species richness over longer time scales. On the other hand, if a proportion of the species actually observed are "tourists" or waifs, the richness estimate will be high because such rare species increase the estimates but are not permanent members of the community being estimated. These two effects will tend to counteract each other. While field guides or checklists may provide accurate lists of species for larger areas accumulated by years of observation, it is difficult to know the "true" species richness of an area small enough to be feasibly sampled in a short time period. Since the true species richness is generally not known in such circumstances, and certainly not for Appalachian spider faunas, the accuracy of the richness estimates can only be assessed indirectly. The agreement among the estimates and the coverage of their associated confidence intervals can be assessed, the estimates can be compared against common sense guesses, checklists, and other studies, and the performance of the estimators on subsets of the data can be assessed. Among the estimators we used, only the continuous lognormal and poisson lognormal are based on models that allow explicit tests of the fit of the model to the data.

Temperate richness estimates.—Five of the six estimators used in this study suggest that the species richness of late summer adult spiders living on the ground and in the understory of this hardwood cove forest was roughly 100–130 species (Table 1). The Poisson lognormal gave consistently high estimates with almost unusably broad confidence limits. The similarity among the former estimates suggests either that they were measuring the true species richness, or that, if biased, they all were affected similarly. The somewhat lower estimates generated for the partitioned data sets of this study reveal that most estimators show substantial negative bias with small sample size (Colwell & Coddington 1994; Chao & Lee 1992), although the confidence intervals usually overlap and the effect is not consistent (Table 1). Since Chao 1, Chao 2, and the jackknife estimators are explicit functions of the number of species observed, such sensitivity is to be expected. This is not necessarily true for the continuous lognormal nor the Michaelis-Menten models, although the former is well-known to require extremely large samples (Magurran 1988). We partitioned the data by date rather than a random selection of samples, and thus our test of the effect of sample size may have confounded the influence of sample size with that of date, collector experience, or climate effects. When sample order was randomized, the same trend was observed (Fig. 3).

Fitting the continuous truncated lognormal model to these sample data was problematic, and different estimates of species richness can be obtained depending on the method used. May (1975) did not recommend fitting the lognormal to data sets containing many fewer than 100 species, and certainly the grouped and log-transformed data in Fig. 1 do not form anything approaching a smooth curve. Although the three Bolivian data sets reported by Coddington et al. (1991) were based on many fewer collecting hours and included fewer adults (Table 5), each fit a lognormal distribution. Since the sampling intensity at the Ellicott Rock site was roughly four times higher than at the Bolivian sites, the relative abundances of species at the Ellicott Rock site are better known. May (1975) pointed out that a lognormal pattern of species abundance is often observed in stable (equilibrium) communities, while disturbed communities will show increased dominance and exhibit instead a log series distribution, but this pattern is far from reliable. Most really diverse communi-

Table 5.—Summary values and richness estimates for the Ellicott Rock and Bolivian sites. Bolivian data from Coddington et al. (1991 and unpubl. data). Sampling intensity is ratio of number of adults to observed species richness. See "Methods" section for explanation of bounds on estimates.

	Ellicott Rock	El Trapiche	Rio Tigre	Cerro Uchumachi
Summary values				
No. of samples	132	51	69	37
No. of adults	1629	875	1109	654
Observed richness	89	191	329	158
No. of singletons	26	89	147	70
% singletons	29	47	45	44
Sampling intensity	18.3	4.6	3.4	4.1
Estimators				
Poisson lognormal	182 ± 126	616 ± 428	691 ± 200	375 ± 188
Chao2	128 ± 40	329 ± 77	583 ± 105	278 ± 73
Chao1	123 ± 35	319 ± 73	506 ± 77	256 ± 63
Jackknife	117 ± 11	283 ± 27	497 ± 40	235 ± 26
Lognormal	114	247	374	191
Michaelis-Menten	104 ± 13	322 ± 104	578 ± 152	277 ± 113

ties are likely to have been so sparsely sampled that either model will fit the data adequately. For example, Turnbull (1966) found a log series fit for spider species abundance data collected from May to September in a north temperate early field succession where dominance by colonizers would be predicted, but the lognormal fits his data also (our calculations).

The greater seasonality of temperate communities should foster narrower, species-specific breeding seasons and thus may cause a sample of adults collected in a short period (a few weeks or less) to mimic the dominance of a low diversity, early successional stage. Just three species (*Micrathena mitrata*, *Micrathena gracilis*, and *Wadotes hybridus*) comprised 29% of all adults in the Ellicott Rock samples. Sampling methodology may also affect the observed species abundance distribution. We may have been biased toward the collection of more apparent (less cryptic and/or more active) species (Stork 1988), especially since the plotless areas sampled in this study were not resampled as they were in the Bolivian study. On the other hand, unbiased samples are unobtainable in practical terms, and our use of experienced collectors is probably no more biased than many other collecting techniques. The ideal is to use an array of collecting techniques that complement each other, rather than trying to design one technique with minimal bias.

According to Chao (1984), her method generates lower bounds on estimates and ought to work best when "most of the information is concentrated on low order occupancy numbers," i.e., when most species in the sample are observed as singletons or doubletons. About 40% of the species were singletons or doubletons in the Ellicott Rock data *versus* an average of 62% in the Bolivian data. Since tropical samples often have a greater proportion of "rare" species than temperate samples, Chao 1 ought to yield better estimates of tropical richness than of temperate richness. However, despite great disparities in the frequency ranges of the temperate versus the tropical data, this estimator clustered about in the middle of other estimates. If poor behavior of an estimator due to violation of assumptions shows up in aberrant values, we did not observe it for Chao 1.

By generating richness estimates from quadrat sampling of a known community of forest floor herbs and shrubs, Palmer (1990, 1991) determined that Heltshe & Forrester's jackknife procedure yielded the best richness estimates out of several estimators tested (although he did not test Chao's estimators). The jackknife method is biased by dominance, but this effect can be reduced by increasing sample size (Heltshe & Forrester 1983). The heavy dominance in the Ellicott Rock samples may have been offset by a large sample size because, although lower than some of the oth-

er estimates, the jackknife estimate is not markedly deviant.

All six of these estimators rely on the proportion of "rare" species, whether the latter, somewhat intuitive, notion is defined more precisely as either uniques or singletons. Common sense suggests that if all species in the sample are known from "many" individuals after much sampling, the sample is probably exhaustive. Therefore, a better understanding of the status of singleton species may help to evaluate and refine estimator performance. (Since propinquity in time and space are highly related in this protocol, species unique to a sample is more a question of patchiness than rarity.) The 26 singleton species collected in our study are distributed rather evenly among collecting methods, families, and guilds (see Appendix). A survey of the taxonomic literature, the third author's multiyear collecting records from this region, and data from a springtime inventory at our study site (Dobyns in press) indicate that 22 of these species are spatially uncommon, i.e., more common either outside the southern Blue Ridge Province (14 species) or in other habitats (6 species) or in the forest canopy (2 species) (see Appendix). The other four singletons are temporally uncommon, i.e., they are species that are common at the site but whose breeding seasons are past.

One can view these rare species as caused by a variety of "edge" effects, of which the most important are habitat, time and method. Habitat edge effects explain the singleton status of canopy species in subcanopy samples, or of species not usually found in mature hardwood forest, but known to be more common elsewhere. Time edge effects explain the four species in fact common at the site, but that were "out of season" at the time we sampled. Finally, method edge effects may explain some of the 14 species not known to be anywhere common in the region. It is a ecological truism that all species must be common somewhere, or, alternatively, that breeding populations have a species-specific spatial structure. Although we cannot be certain, we doubt that few of these 14 species naturally occur at such low densities that nearest neighbor distances are greater than 100 meters. More likely, these "rare" species occur in the area we sampled, but have natural histories that make them difficult to collect by the methods we used. Nevertheless, although "edge" effects may explain rare species to some extent, they still are valid indicators that an inventory is incomplete.

The richness estimates derived from this study must be interpreted critically due to the spatial and temporal (seasonal) bias of the sampling methods utilized. This study estimated only that proportion of the total fauna that was 1) available to the collecting methods used and 2) adult during the course of the study. Perhaps the most significant omissions are the canopy fauna and those species present only as juveniles. Examination of about 4200 of the 5037 juveniles (76% of all specimens collected in the samples) revealed that between 25–40 species were not represented by adults in any of the samples. As noted above, richness estimates are biased upwards by inclusion of "tourist" or waif species that may be ecologically "out of place" or merely passing through the site, and they are biased downwards by low sampling effort and phenology. However, if one presumes that the total fauna available to the methods during the collecting period was observed either as adults or juveniles, then the true species richness of the site was 114–129 species. The estimates of Table 1 all agree fairly well with this common sense figure.

On the other hand, the behavior of all estimators in Fig. 3 is reason to believe that the true species richness is still underestimated. Colwell & Coddington (1994) reported one data set in which even the empirical curve reached an obvious asymptote. As expected, "good" estimators achieved this asymptote (or very close to it) much sooner than the empirical curve. The sampling intensity of that data set was over 30:1; but the Ellicott Rock inventory was 18:1, and the three Bolivian inventories were less than 4:1. If sampling intensity is a rough guide to required effort, then it appears that the 10:1 figure guessed at by Coddington et al. (1991) is seriously low.

The only previous study of spider species richness in a southern Appalachian forest is that of Coyle (1981). Using aerial hand (2.25 h), ground hand (2.25 h), Tullgren litter (ten 0.25 m^2 samples), sweep net (about 2 h), and pitfall trap (eight traps for 15 weeks) methods between June and October, he collected 217 individuals and 51 species as adults (and 9 more as juveniles) from a mature mixed pine-

hardwood site in the Ellicott Rock Wilderness Area, and about 5 km from the site we sampled. Only 29 species, or 33% of the species present in our total sample, are common to his sample and ours. Both samples are similar in the percent of sampled species of adults in three (ground web-builders, aerial web-builders, and aerial hunters) of the four guilds, but the Coyle sample had 18% ground hunters *versus* 9% in ours (9 of 51 *versus* 8 of 89 species, respectively). The greater duration of the Coyle study and his low ratio of hand collecting effort to pitfall trap effort (which biased his study in favor of ground hunters) help account for these differences.

Comparison of temperate and tropical richness estimates.—It is no surprise that the species richness estimates for tropical sites (Coddington et al. 1991; Silva & Coddington in press) are much greater than for the temperate (Ellicott Rock) site (Table 5). Of the tropical sites, Rio Tigre was most nearly comparable in elevation to the Ellicott Rock site (500 m *versus* 800 m). Comparison of observed species richness indicates that Rio Tigre had 3.7 times more species than Ellicott Rock, but comparison of the six estimated species richness values indicates ratios from 3.8–5.6. Comparing Georgia to Bolivia is not the point, but rather that comparisons of raw sample data can mislead. In this case, the lower intensity tropical sample apparently accessed a much smaller proportion of the total fauna present. Use of statistical procedures may emend such biased comparisons and enable better comparison of the results of inventories that differ in method, circumstances and completeness. This higher tropical species richness resembles the north temperate to tropical latitudinal gradient observed for many other taxa (Fischer 1960; Ehrlich & Wilson 1991; Platnick 1991). Interestingly, all the estimators for the tropical data sets show the same rank order. With the exception of the species accumulation curve, the same ranking is repeated in the temperate data set. This rather startling consistency in rank order among estimators suggests a systematic bias with respect to each other (and therefore with respect to the true richness), at least for the data sets tested thus far. It therefore remains to be demonstrated, perhaps through simulation studies, which estimator most accurately tracks the true richness.

Effects of method, time of day and collector on results.—Although some methods (aerial and ground) were more productive than others (beating and litter), the Bray-Curtis indices and the numbers of collected species unique to each method suggest that each method is sampling a distinctly different array of species. Of course, species that are singletons cannot appear in more than one sample, and these may artificially inflate the distinctiveness suggested by such comparisons. Although aerial collecting and beating both accessed similar vegetative habitats, aerial sampling accessed larger spiders (araneids) while beating accessed a higher proportion of smaller cryptic species (especially linyphiids; see Appendix) which are likely to be overlooked during aerial hand collection. Ground hand collection accesses far more microhabitats than does litter collection, but is less likely to sample the smallest-bodied litter-dwelling species. The extensive use of aspirators in ground hand collection probably reduces this difference between the two methods in the size of the spiders collected. It is logical to expect that methods which depend heavily on visual searching (aerial and ground) are biased against small-bodied species. The higher ratios of large to small spiders in the aerial and ground samples compared to beating and litter samples, respectively, conform to that prediction. Additional evidence of this bias is the high female to male ratio (13.5:1) for aerial collections of three common species with much larger females than males (*Micrathena gracilis*, *Micrathena mitrata*, and *Spintharus flavidus*) and the much more normal ratio (1.5:1) for ground collections of large-bodied species with little sexual size dimorphism (*Wadotes hybridus*, *Wadotes bimucronatus*, and *Gladicosa gulosa*). As Poole (1974) has noted, the whole question of "true" relative abundance of species in nature as compared to relative abundance in samples is nearly insoluble, however fundamental it may be to assessing bias.

The especially high variability of the litter sample data may be the result of heterogeneity in spider distribution, variation in litter depth (Uetz 1975), or variation in Tullgren funnel technique (funnels were sometimes overloaded and the litter not allowed to dry completely). Sampling equal volumes (rather than areas) of litter, placing a constant and moderate

volume in each funnel and continuing the extraction process until the litter is completely dry should reduce this variability and make comparisons between sites more meaningful. Sorting spiders from litter by hand in the field on a white tray for one hour might allow litter to be analyzed as a time-based method, but this probably would not be as efficient as Tullgren funnel extraction and would be less likely to capture very small spiders.

Although time of day had no significant effect on the number of adults and number of species collected, and Bray-Curtis indices indicated that time of day affected the taxonomic composition of samples less than method did, the relatively large number of species unique to either day or night samples indicates that both night and day collecting may be desirable if the sampling is to approach closely the real species richness of the site. These data (see Appendix) support the generalization that many spider species are either predominantly night or day active. *Wadotes hybridus*, *Gladicosa gulosa*, *Mimetus interfector*, *Thiodina sylvana*, *Spintharus flavidus*, and *Hyptiotes cavatus* were species whose collection was strongly skewed toward the night (nocturnally active species), while *Micrathena gracilis*, *Ceraticelus fissiceps*, *Ceratinopsidis formosa*, and *Gonatium crassipalpum* were far more abundant in day collections (diurnally active species). *Micrathena mitrata* was the only commonly sampled species that appeared to be equally active both night and day. Unlike these results, night sampling in the Bolivian forests was significantly more productive (numbers of adults and species per sample) than day sampling (Coddington et al. 1991), supporting the oft quoted generalization that most kinds of spiders are most active at night, and perhaps that diurnal predation pressure may be more intense in tropical than in temperate forests.

We should note, however, that collector fatigue may have markedly reduced the productivity of night collecting in our study. While the collectors in the Bolivian study in general collected only 5 one-hour samples in any 24 h period, the temperate sampling was done primarily on weekends with as many as 10 h of sampling per collector in a 24 h period. For example, the total numbers of adults collected by the three collectors on the night of 14 September were 48 for hour 1, 51 for hour 2, 36 for hour 3, and 22 for hour 4; and the plan to collect for another hour was aborted due to fatigue.

The data analysis suggests that naive and experienced collectors do differ in their abilities and that the sampling time required for a richness survey can be reduced by selecting particularly able collectors. We suspect that the collectors in the Bolivian study, who averaged 16.4 adults per sample (Coddington et al. 1991), would have averaged significantly more than the 12.2 adults per sample average productivity of the Ellicott Rock team because the most experienced Ellicott Rock collector almost equalled the Bolivian average but had far less spider-collecting experience than four of the five collectors in Bolivia. However, this study and the Bolivian study both showed that the sampling productivity of inexperienced collectors can improve so that they soon became statistically indistinguishable from the more experienced collectors. This improvement in collector performance is encouraging since it suggests that it is possible to train naive collectors rather quickly and thus to implement efficient, long-term, continuous monitoring in the tropics.

Collector (and method) productivity may have been affected by climate-induced changes in adult spider activity and/or abundance. The reduced average sample size during period 4 (Table 4) was probably a result of a diminished number of active spiders due to markedly colder and windier weather and not a reduction in collector performance.

Recommendations for future research.—Since sampling protocols should access all components of a fauna without bias, and since the protocol used by Coddington et al. (1991) under-samples the litter fauna, methods that access this fauna (litter extraction, pitfall traps) should be added wherever feasible. Hand sorting of litter for one hour on a tray would be logistically easier in remote areas due to the scarcity of electricity, but Tullgren funnel extraction may be more productive and a study is needed to test that hypothesis; either way it would be more informative to also record the volume of litter processed. We have shown that beating can be performed as a time-based sampling method to make data analysis more straightforward. This study provides some, albeit weak, evidence for the importance of night sampling; and it suggests that sampling should be limited to 5–6

sample hours per 24 hour period to minimize the effects of collector fatigue. Additional sampling of this and other hardwood coves in the southern Appalachians should be undertaken in September, in May, and in July: 1) to see if the species richness estimates of 104–128 are repeatable, 2) to explore the effect of season on richness estimates (see Dobyns in press), 3) to compile a more accurate species list to which the performance of richness estimators can be compared, and 4) to facilitate the identification of juveniles so that the effect of their inclusion on species abundance distributions and richness estimates can be studied. Simultaneous plotless and quadrat sampling studies should be performed to compare plotless richness estimates with those based on 1) pooled quadrats (Pielou 1975) and 2) species-area relationships (Palmer 1990, 1991). The hypothesis that repeated (intensive) sampling in a plot will collect more covert species than does non-repetitive collecting requires testing (see Dobyns in press). Statistical research to develop confidence intervals for species accumulation curves and lognormal estimates is required, as is further study of the dependence of estimates on sample size and their performance on data sets that display different degrees of ecological dominance (i.e., range of frequencies). Spider richness studies should be located at sites where other animal or plant diversity plots already exist so that the correlation between spider richness and the richness of other taxa can be explored.

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Appendix.—Species and number of adult spiders collected in Ellicott Rock species richness study. Collection method and time of day indicated (D = day, N = night). Guild designation: A = aerial, G = ground, W = web building, H = hunting. Status of singleton species: R = rare in southern Blue Ridge Province; U = uncommon to moderately common in southern Blue Ridge Province; J = juveniles common in samples (adults common at another time of year); P = at periphery of its geographic range; H = common locally in other, usually more open, habitats; C = probably common in forest canopy (Coddington 1987).

		Collection method							Singleton status
		Aerial		Ground		Beating			
Taxon	Guild	D	N	D	N	D	N	Litter	
Agelenidae									
Agelenopsis pennyslvanica	AGW	10	2	4	3	1	1		
Calymmaria cavicola	GW			22	40				
Cicurina arcuata	GW			3	7			12	
Cicurina breviaria	GW			6	3			2	
Cicurina sp. A	GW			2					
Cicurina sp. B	GW			1					R
Coras aerialis	AW		1						U
Coras taugynus	GW			2	9				
Cybaeus silicis	GW		2	6	4				
Wadotes bimucronatus	GW			28	41			5	
Wadotes hybridus	GW			18	101			3	
Amaruobiidae									
Callioplus armipotens	GW			1	2			4	
Anyphaenidae									
Anyphaena pectorosa	AH						1		U
Wulfila alba	AH						1		U
Araneidae									
Araneus cingulatus	AW		1						C
Araneus marmoreus	AW	25	10				1		
Araneus niveus	AW		1						C
Araneus nordmanni	AW	17	6	1		3	1		
Araneus pegnia	AW		1						H
Araneus saevus	AW		1						P
Araneus thaddeus	AW	1	5			2			
Mangora maculata	AW	1				1			
Metepeira labyrinthea	AW	7	1				1		
Micrathena gracilis	AW	111	39	1	1	4	1		
Micrathena mitrata	AW	77	99	1	2	1	6		
Micrathena sagittata	AW	1							U
Neoscona arabesca	AW	1							H
Neoscona domiciliorum	AW	18	17	1	1	2	1		
Neoscona hentzi	AW	1							U
Wixia ectypa	AW		3			2	2		
Clubionidae									
Clubiona spiralis	AH		1						P
Clubionoides excepta	AH	1	1		1	5	3		
Phrurotimpus alarius	GH			1				1	
Scotinella redempta	GH			4				2	
Trachelas similis	AH		2			3	4		
Trachelas sp. A	AH		1						R
Ctenidae									
Anahita punctulata	GH				1				J
Hahniidae									
Neoantistea agilis	GW			1	3				

Appendix.—Continued.

		Collection method							Singleton status
		Aerial		Ground		Beating			
Taxon	Guild	D	N	D	N	D	N	Litter	
Hypochilidae									
Hypochilus pococki	GW	2		11	3				
Leptonetidae									
Leptoneta gertschi	GW			13	7			19	
Linyphiidae									
Bathyphantes albiventris	GW			1	1				
Centromerus denticulatus	GW							2	
Ceraticelus carinatus	GW			1			1	36	
Ceraticelus fissiceps	AGW			3		51	18	2	
Ceraticelus minutus	GW							3	
Ceratinopsidis formosa	AW	3	1	1		53	13	1	
Drapetisca alteranda	AW	11	8			2			
Erigone autumnalis	GW					1			J
Frontinella pyramitela	AW	6	4	1					
Gonatium crassipalpum	AW					15	2	1	
Graphomoa theridioides	GW	1		50	32		1		
Lepthyphantes sabulosa	GW			4	6			6	
Lepthyphantes sp. A	GW			1	2				
Lepthyphantes turbatrix	AGW		1		2				
Meioneta micaria	GW			1					H
Meioneta sp. A	AW		1						R
Neriene radiata	AW	2							
Neriene variabilis	GW			2	1				
Pelecopsidis frontalis	GW			1					R
Scylaceus pallidus	GW							1	P
Walckenaeria brevicornis	GW							2	
Lycosidae									
Gladicosa gulosa	GH		7	3	61		3		
Pirata montanus	GH			6	1			1	
Mimetidae									
Mimetus interfector	AH	1	5		1		1		
Mysmenidae									
Mysmena guttata	GW							1	J
Salticidae									
Eris marginata	AH	1		1		8	6		
Habrocestum parvulum	GH			4				3	
Habrocestum pulex	GH	1		2					
Maevia intermedia	AH	1	1		1	8	2		
Metaphidippus protervus	AH					3			
Thiodina sylvana	AH					1	8		
Tetragnathidae									
Glenognatha foxi	AW					1			H
Leucauge venusta	AW	9	5	2		1			
Meta menardi	AGW			1	1				
Tetragnatha elongata	AW			1					H
Theridiidae									
Argyrodes trigonum	AW	2	1		1	1			
Euryopis funebris	AW		1			1			
Paratheridula perniciosa	AW					1			P
Pholcomma hirsuta	GW			1				3	

Appendix.—Continued.

Taxon	Guild	Collection method							Sin-gle-ton status
		Aerial		Ground		Beating		Litter	
		D	N	D	N	D	N		
Spintharus flavidus	AW	1	44		4	11	18		
Theridion albidum	AW	2			1				
Theridion flavonotatum	AW	1				1			
Theridion lyricum	AW		7		4	5	5		
Theridula opulenta	AW						3		
Theridiosomatidae									
Theridiosoma gemmosum	AGW				1				J
Thomisidae									
Misumena vatia	AH					1			H
Xysticus fraternus	GH				1	1		1	
Uloboridae									
Hyptiotes cavatus	AW	7	35	8		5	9		
Uloborus glomosus	AW				1				U
Totals		322	315	222	351	195	113	111	

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METABOLIC RATES OF RESTING SALTICID AND THOMISID SPIDERS

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ABSTRACT. Rates of metabolism of jumping and crab spiders were evaluated to determine if life-style characteristics are associated with rates of energy expenditure in these 'sit-and-wait' predators. Resting rates of oxygen consumption were measured under standardized conditions in nine species of salticid and three species of thomisid spiders. These rates and those previously reported ranged from 50–70% of that expected for their size in these families. They are similar to those of other families of spiders with similar modes of prey capture, life span, and distribution. No significant differences in this measure were detected between the two families.

Rates of energy expenditure in spiders exhibit much variation, and it has been my goal to document and account for this diversity (Anderson 1970; Anderson & Prestwich 1982; Anderson 1994). As in most organisms (Peters 1983), body size is the major source of variation in energy expenditure in spiders (Humphreys 1977; Greenstone & Bennett 1980; Anderson & Prestwich 1982). Nonetheless, considerable variation in this measure remains after adjustment for size. Most spiders have low rates of metabolism (~ 50% of expected for their size) compared to other ectothermic poikilotherms. This feature is considered an adaptation to an unpredictable food supply (Anderson 1970; Greenstone & Bennett 1980) in these predators. This interpretation is consistent with the observation that those species with very low metabolic rates, i.e., less than 50% of expected for their size, live much longer than one year, often colonize marginal habitats, and are restricted in distribution to lower latitudes (Anderson & Prestwich 1982; Anderson 1994). Conversely, the high rates of metabolism (~ 100% of expected) found in orb-weavers and comb-footed spiders are associated with high reproductive rates, rapid growth, high population densities, and widespread distribution (Anderson 1994).

The proposed associations between energetics and biology were made by measurement of rates of respiratory gas exchange in resting spiders. Since spiders are inactive most of the time, this measurement represents a significant fraction of their total energy requirement (Andrews & Pough 1985). Interpretation of such comparisons is complicated because any given trait may reflect selection associated with environmental constraints as well as phylogenetic affiliations (Huey 1987; Wang & Abe 1994). Huey (1987) recommends that studies of closely related species most effectively resolves such ambiguities. Conversely, Andrews & Pough (1985) suggested that associations between energy metabolism and ecology of a species could be evaluated from data obtained on species with similar ecological characteristics but who differ phylogenetically.

I selected species in the families Salticidae and Thomisidae as a compromise between these two recommendations. There is little information available relating to energetics in these important taxa. Both families constitute a large and important component of the spider fauna. They contain 4,000 and 2,000 described species, respectively, out of a total 34,000 spiders in this order and are cosmopolitan in distribution (Coddington & Levi 1991). Obviously they differ in phylogeny as they are separated at the familial level. The two families are, however, closely related (Coddington & Levi 1991). They differ greatly in morphology but are similar in certain particulars: both are diurnally active and do not use a web to capture prey. Jumping spiders have a better sense of vision and often pursue prey over some distance. Larger spe-

cies are stationary: from their vantage point they visually scan the environment for prey (Enders 1975; Richman & Jackson 1992). Smaller jumping spiders spend much of their time moving and then stopping to look for prey (Enders 1975). In contrast, crab spiders are relatively stationary and ambush prey coming in close proximity. As such, thomisids reside at locations where prey commonly occur, i.e., flowers, tree trunks, stems of vegetation, and in litter (Dondale & Redner 1978; Morse 1983). Most exhibit cryptic coloration (Gertsch 1979).

My aim here is to measure resting rates of metabolism and use these data to assess the validity of the relationship between life-style characteristics and energetics. I predict the rates of both jumping spiders and crab spiders will be *ca.* 50–60% expected for their size. I base this prediction on the notion that they share certain characteristics with other spiders whose rates of metabolism have been reported (Anderson 1970; Greenstone & Bennett 1980). Their life-style characteristics are more similar to wolf-spiders (Lycosidae) than they are to orb-weaving spiders (Araneidae) and comb-footed spiders (Theridiidae). Comparisons between the salticids and thomisids might also be instructive. Enders (1976a, b) has shown that thomisids have larger clutch sizes and percent growth increases during molting than salticids. This suggests that thomisids would have a higher rate of metabolism. Conversely, the greater activity of salticids presumes a relative larger muscle mass which in turn might be associated with a higher rate of metabolism even at rest. Comparison of data on energetics from species in these two families might provide answers to these questions.

METHODS

Animals.—Species selection was based on availablity and ability to identify specimens. The three thomisid spiders obtained were *Misumenoides formosipes* (Walckenaer 1837), *Misumenops celer* (Hentz 1847) and *Xysticus funestus* (Keyserling 1880). The salticids studied were *Eris marginata* Peckham 1886, *Marpissa bina* Hentz 1846, *Metaphidippus galathea* (Walckenaer 1837), *Phidippus audax* (Hentz 1845), *P. clarus* Keyserling 1885, *P. pulcherrimus* Keyserling 1885, *Sarinda hentzi* Banks 1913, *Thiodina sylvana* (Hentz 1885) and *Zygoballus rufipes* (Peckham & Peckham 1885).

All spiders were collected from locations around Gainesville, Florida. They were kept individually in plastic containers under ambient photoperids at room temperatures ranging from 22–24 °C. Specimens were fed weekly on a variety of prey as recommended by Greenstone (1979) and Uetz et al., (1992). These included adult fruit-flies and different life stages of crickets and mealworms. Some spiders were deposited as voucher specimens in the collections of the Division of Plant Industry of the Florida Department of Agriculture and Consumer Services at Gainesville when the study ended. The remainder were released at sites where collected.

Rates of metabolism.—Rates of metabolism were measured at 20 °C and 100% relative humidity to make comparisons with published data. Although 20 °C may seem unrealistic for this area, it is the average yearly temperature in northern Florida (Bradley 1972). This temperature is approached during evening hours even in summer. The rates of metabolism of both salticids and thomisids were measured overnight when these animals are normally inactive and about one week after their last meal (Anderson 1970).

Rates of oxygen consumption ($\dot{V}O_2$) were used as measures of metabolic rate. Disposable syringes of 30 or 60 cm^3 capacity, depending upon animal size, were used as 'closed system' metabolic chambers (Vleck 1987). The syringes were fitted with three-way valves which allowed sealing their contents from the atmosphere during measurement and gas sampling to determine O_2 composition. A small piece of moistened filter paper was added to each syringe to hold relative humidity at 100% during incubation. Spiders were weighed and placed individually within syringes. The syringes were ventilated with room air prior to adding spiders. The syringes were closed to the atmosphere and placed in a darkened incubator kept at 20 °C. Three empty syringes served as controls for each set of measurements. The length of incubation was controlled such that the O_2 did not decrease more than 0.5% to preclude the effects of abnormal gas concentrations on respiration. Previous tests indicated the syringes do not leak (Anderson et al. 1989) under the conditions and times used here. The O_2 frac-

Table 1.—Relationship between oxygen consumption and live body mass at 20 °C. Dimensions for $\dot{V}O_2$ and M are μLO_2/hr and mg, respectively. The regressions are based on log transformed data and are all significant at P = 0.004 or less.

Family Species	n	Range in body mass (mg)	$\dot{V}O_2 = aM^b$ a	b	Reduced major axis slope	r^2	SEE
Thomisidae							
Misumenoides formosipes	42	11–154	0.62	0.70	0.90	0.60	0.132
Misumenops celer	63	4.0–76	0.52	0.71	0.98	0.53	0.138
Xysticus funestus	61	4.8–55	0.29	0.88	0.98	0.82	0.113
Salticidae							
Eris marginata	36	3.9–43	0.44	0.78	1.10	0.48	0.199
Metaphidippus galathea	24	2.6–14	0.63	0.48	0.84	0.29	0.129
Phidippus audax	41	3.9–338	0.50	0.81	0.83	0.93	0.121
Phidippus pulcherrimus	131	12–196	0.34	0.85	0.99	0.73	0.116
Thiodina sylvana	15	24–110	0.30	0.91	1.06	0.71	0.127

tion of a minimal 20 cm³ sample from a syringe was determined at the end of incubation using an Ametek S-3A O_2 Analyzer (see Anderson et al. 1989 for details). Rates of metabolism (in $\mu L\ O_2$/hr) were calculated using the equation modified from Vleck (1987):

$$\dot{V}O_2 = \frac{V(F_{IO2} - F_{EO2})}{(1 - F_{EO2})\cdot t}$$

Here V is the initial volume of dry, CO_2-free air in the syringe at STP; F_{IO2} and F_{EO2} are O_2 fractions within the syringe at the beginning and end of incubation, respectively; and t is the length of incubation in hours.

Analysis and comparison of rates of metabolism.—Where possible, i.e., species with large range in body size, I analyzed the data to describe the relationship between metabolism and body size to provide a reference for making comparisons between spiders of different mass (Packard & Boardman 1987; Anderson 1994). I did evaluate whether the untransformed data provided a better fit than log transformed data. The latter provided a better fit in six of the eight species. Since the fit was only nominally better using the untransformed data I used log transformed data to calculate a and b in the allometric equation

$$\dot{V}O_2 = aM^b$$

Here a is a coefficient of proportionality (it provides an estimate of the rate of metabolism for a spider of one unit mass), b is the scaling exponent, and M is body mass. Given the conceptual and statistical problems associated with allometric relationships, I followed the suggestions of Smith (1984) and LaBarbera (1986) and reported the range in body mass, standard errors of estimates (SEE), coefficients of determination (r^2), and reduced major axes slope (RMA) for each regression. I used a P value of $\leq$ 0.05 as the signficance level for statistical decisions.

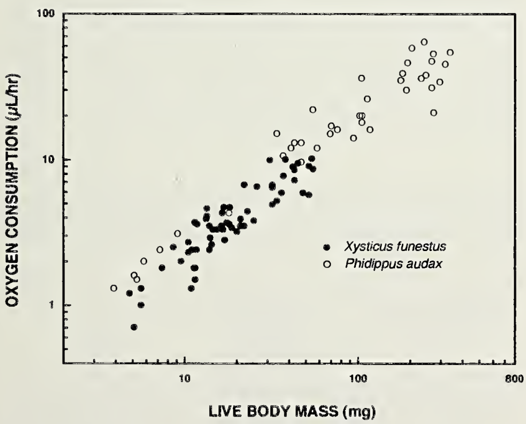

Figure 1.—Relationship between oxygen consumption and live body size in *Xysticus funestus* and *Phidippus audax*.

RESULTS

The parameters describing the relationship between rates of metabolism $\dot{V}O_2$ and body size are reported in Table 1 for those species whose data sets were appropriate for regres-

Table 2.—Oxygen consumption of some adult salticid spiders at 20 °C. Reported values are means ± SD.

Species	n	Live body mass (mg)	$\dot{V}O_2$ (μL O_2/hr)
Marpissa bina	3	168 ± 51	26 ± 2.6
Phidippus clarus	7	260 ± 74	46 ± 22
Sarinda hentzi	2	4.6 ± 1.8	2.0 ± 0.8
Zygoballus rufipes	2	3.0 ± 0.3	0.6 ± 0.1

sion analysis. The variation in proportionality coefficient (a) is inversely correlated to scaling exponent (b) illustrating the mathematical interdependence of these variables (Gould 1966; Anderson 1994). Figure 1 depicts the relationship between $\dot{V}O_2$ and body size during ontogeny in a thomisid, *Xysticus funestus*, and a salticid, *Phidippus audax*. The representation is typical of this relationship within a spider species in showing that much variation exists at any one body size (see also Anderson 1994) even though the figure represents logarithmically transformed data. Rates of metabolism for adult salticids whose weight ranges and sample size precluded regression analysis are reported in Table 2.

DISCUSSION

I compared rates of metabolism of thomisids (Table 3) and salticids (Table 4) with an empirical standard (Hemmingsen 1960) to assess the validity of my prediction that these spiders should have rates of energy expenditure of about 50% expected for their size. These comparisons are made on the basis of adult-sized females of each species. Selection pressures associated with energetic constraints are different for the two sexes. Males are relatively short-lived and the energy used in gamete production is small. The high energy demands associated with courtship behavior of males is important, but only in a proximal sense. Females must obtain energy at rates necessary to maintain their larger body size over a longer life span as well as for the higher energetic cost of gamete production. I used proportionality coefficients (a) and scaling exponents (b) to estimate $\dot{V}O_2$ for the largest individual for each species listed in Table 1 or the average $\dot{V}O_2$ of the adult spiders listed in Table 2 as the basis for comparison. The comparison also includes data from published studies normalized to 20 °C using a Q_{10} of 2.0. The comparisons agree with predictions. The observed rates of metabolism of the crab-spiders averaged 53% (SD ±8) of expected for their size while those of the jumping spiders averaged 67% (SD ±18) of expected. This agreement supports the view that energy metabolism is related to a species' natural history. There are at least two other families, the Clubionidae and Gnaphosidae, whose members share certain characteristics with thomisids and salticids. The similarity in length of life-cycle, relative rates of reproduction, and method of prey capture suggest their rates of metabolism would be similar. Published values (Greenstone & Bennett 1980) for specimens in these families are *ca.* 30–40% but are based on only two specimens. More work is necessary to validate this prediction.

Table 3.—Comparative rates of metabolism of adult crab spiders. Expected values were calculated using Hemmingsen's (1960) equation: $\dot{V}O_2 = 0.82\ M^{0.75}$. Data for *'Misumenops species'* are from Greenstone & Bennett (1980).

Species	Adult live mass (mg)	Observed $\dot{V}O_2$ (μL O_2/hr)	Expected $\dot{V}O_2$ (μL O_2/hr)	$\frac{OBS}{EXP}$
Misumenoides formosipes	154	21	36	0.58
Misumenops celer	76	11	21	0.52
Misumenops species	34	5.0	12	0.42
Xysticus funestus	55	9.9	17	0.58

Table 4.—Comparative rates of metabolism of adult jumping spiders. Expected values were calculated using Hemmingsen's (1960) equation: $\dot{V}O_2 = 0.82\ M^{0.75}$. Data for *M. bivittatus, M. vitis,* and *P. johnsoni* are from Greenstone & Bennett (1980). Those for *P. otiosus* and *P. regius* are from Anderson (1970).

Species	Adult live mass (mg)	Observed $\dot{V}O_2$ (μL O_2/hr)	Expected $\dot{V}O_2$ (μL O_2/hr)	OBS/EXP
Eris marginata	43	8.3	14	0.59
Marpissa bina	168	26	38	0.68
Menemerus bivittatus	28	8.8	10	0.88
Metaphidippus galathea	14	2.2	5.9	0.37
Metaphidippus vitis	5.7	2.3	3.0	0.77
Phidippus audax	338	56	65	0.86
Phidippus clarus	260	46	53	0.87
Phidippus johnsoni	173	20	39	0.51
Phidippus otiosus	337	48	65	0.74
Phidippus pulcherrimus	196	30	43	0.70
Phidippus regius	568	54	95	0.57
Sarinda hentzi	4.6	2.0	2.6	0.77
Thiodina sylvana	110	22	28	0.79
Zygoballus rufipes	3.0	0.6	1.9	0.32

Comparisons between thomisids and salticids are equivocal. Although rates of metabolism of the salticid species appear higher than those of thomisids of comparable size (Fig. 2), the difference is not significant. I used analysis of covariance (Packard & Boardman 1987) to compare rates of metabolism of adults (Tables 3, 4) using both species ($P \sim 0.21$) and genus ($P \sim 0.27$) as independent statistical units. I am aware of the argument that lower taxonomic units are probably not statistically independent as the trait in question has not evolved independently (Harvey & Pagel 1991). The small number of species, especially thomisids, precluded meaningful application of the method (program supplied and described by Purvis 1991) of 'Independent Contrasts' to partition out the effect of phylogeny. The question therefore is not resolved. Nonetheless the question has been posed and its answer awaits futher data. The possibility exists that these low rates of metabolism are plesiomorphic in spiders (Coddington & Levi 1991) and probably in other predatory arachnid groups. The depression of rates of metabolism in 'sit-and-wait' predators reaches its ultimate in ticks. Lighton & Fielden (1995) reported rates only 12% of expected in these animals when compared to other arthropods including spiders.

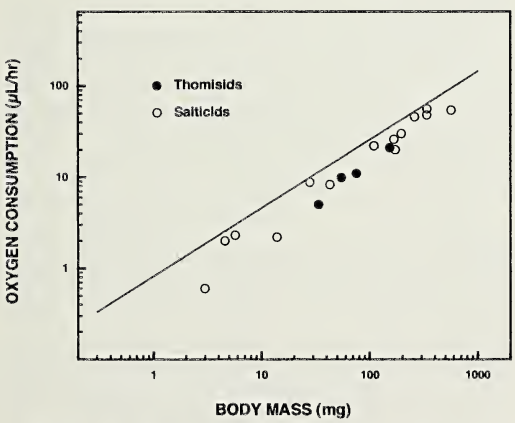

Figure 2.—Relationship between oxygen consumption and live body size in adult salticid and thomisid species. Solid line represents Hemmingsen's (1960) equation for this relationship in ectothermic poikilotherms.

The many reported differences between members of these two morphologically distinct families have a smaller energetic impact than does the association with the low rates of metabolism associated with the sit-and-wait foraging pattern common to both families. This association between foraging pattern and energetics has also been found in other ectothermic predators such as snakes (Cruz-Neto & Abe 1994) thus supporting this notion.

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SPIDERS ASSOCIATED WITH EARLY SUCCESSIONAL STAGES ON A VIRGINIA BARRIER ISLAND

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ABSTRACT. Communities consisting of small shrubs and larger pre-thicket plants of *Myrica cerifera* (Myricacae) and *Baccharis halmifolia* (Asteraceae) were sampled by sweepnet in early June, July and August of 1995 to estimate the density and diversity of spider communities associated with these shrubs during early successional stages of thicket development. This was initiated as part of a larger study intended to determine establishment patterns of these two shrubs in graminoid dominated swales (low-lying wetlands between dune ridges). The species *Hentzia palmarum* (Hentz 1832), *Eris flava* (Peckham & Peckham 1888) (Araneae, Salticidae) and *Misumenops celer* (Hentz 1847) (Araneae, Thomisidae) were common to both *Myrica* and *Baccharis*; however, densities differed between shrubs. *Habronattus agilis* (Banks 1893) (Salticidae) was uncommon and only found on *Myrica* while the infrequent species *Poultonella alboimmaculata* (Peckham & Peckham 1883) (Salticidae) was only found on *Baccharis*. The greatest differences in spider densities were between the early transitional swale site and the developing thicket (later transitional swale) site. Insect communities sampled had greater observed differences in structure between the two shrubs than were found with spiders.

Much of the work dealing with spiders and spider assemblages has focussed on the role of spiders as predator control agents in both natural and man-altered ecosystems (Reichert & Lockley 1984; Nyffeler et al. 1987; Reichert & Bishop 1990). Less-studied aspects of spider ecology are the habitat requirements of species and the dynamics of guild structure in natural habitats.

While many spiders may be generalist predators, many species may have fairly strict habitat requirements. Species may segregate by habitat or be cryptically adapted to hunt on selected plant substrates (Döbel et al. 1990; Coetzee et al. 1990; Cutler 1992; Cutler & Jennings 1992). Spiders in selected habitats may also utilize woody plants as habitat islands (Ehmann 1994).

On mid-Atlantic barrier islands, vegetation behind the foredune grades from xeric grass dominated communities into graminoid dominated swales. Established swales are soon colonized by waxmyrtle (*Myrica cerifera*) and groundsel tree (*Baccharis halmifolia*). These plants in the colonizing swale are found as widely scattered small individuals or as part of larger clumps containing both *Myrica* and *Baccharis*. As the island ages, *Myrica* and *Baccharis* in the older swales gradually develop into a thicket. Immature thickets contain large *Myrica* (1–2 m canopy spread) and scattered smaller (0.25–1 m canopy spread) individuals of both *Myrica* and *Baccharis*. While many *Myrica* plants are large, there is no continuous canopy coverage as is found in the mid-island or bay-side thickets (Young et al. 1995).

In the most recently established swale, many individuals of both *Myrica* and *Baccharis* show visible signs of herbivory (pers. obs.). Such herbivory may alter the ultimate composition of the thicket community by restricting growth of certain plants or by eliminating individuals (Kraft & Denno 1982; Krischik & Denno 1990). Spiders associated with *Myrica* and *Baccharis* may in turn alter insect distribution and density such that impact of herbivory may be lessened and plants are better able to compete (Crawley 1983; Reichert & Lockley 1984).

The purpose of this study was to 1) investigate spider species and composition of assemblages associated with small and pre-canopy-closure plants of *Myrica cerifera* and *Baccharis halmifolia*, and 2) estimate seasonal

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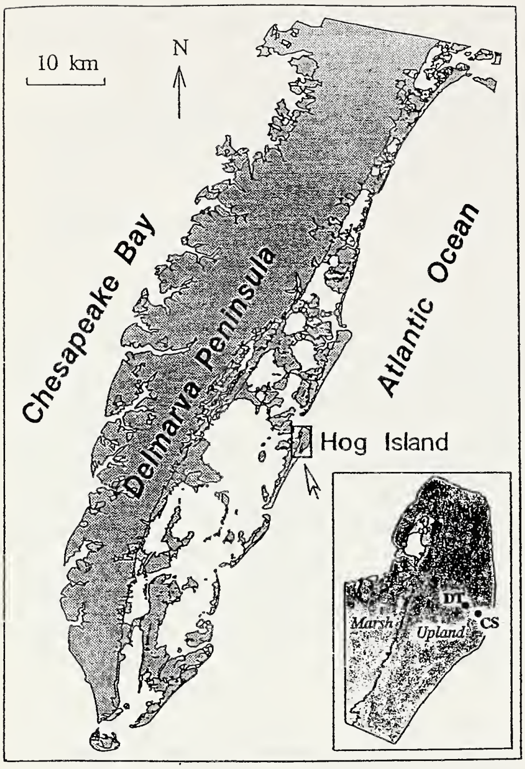

Figure 1.—The Virginia portion of the DelMarVa peninsula and the associated barrier islands which make up the Virginia Coast Reserve. The two field sites, developing thicket (DT) and colonizing swale (CS), are shown on the insert depicting the north half of Hog Island.

Figure 2.—Depiction of the developing thicket (on the left) and the colonizing swale (right) showing the relative density of plants and pattern of sweep sampling. *Baccharis* plants are shown in solid black. Large and medium *Myrica* plants are shown with crosshatching; small plants are left clear.

patterns of distribution and density of the most common spiders and potential prey insects on these shrubs. This study represents a portion of a larger study designed to determine the dynamics of colonization of *M. cerifera* and *B. halmifolia* on newly established barrier island swales.

METHODS

Study sites.—Field work was conducted on Hog Island (37°40′N, 75°40′W). This island is part of the Virginia Coast Reserve and is the primary LTER site within the VCR (Dueser et al. 1976; Hayden et al. 1990). The north end of Hog Island is actively accreting while the south end of the island is eroding. Shrub thickets are well developed along the middle of the island and along the bay side. Due to the creation of new swales at the north end, new thickets are forming east of the mid-island thicket (Young et al. 1995). Therefore, to estimate spider and insect densities and distributions on developing shrub thickets on barrier islands, four distinct sites were selected which included developing shrub thicket and early transitional swale. These communities are separated by a well developed xeric dune ridge (Figs. 1, 2).

Spiders and insects were collected with a sweepnet. Unidentified species were preserved in alcohol and sent to Bruce Cutler at the University of Kansas for identification.

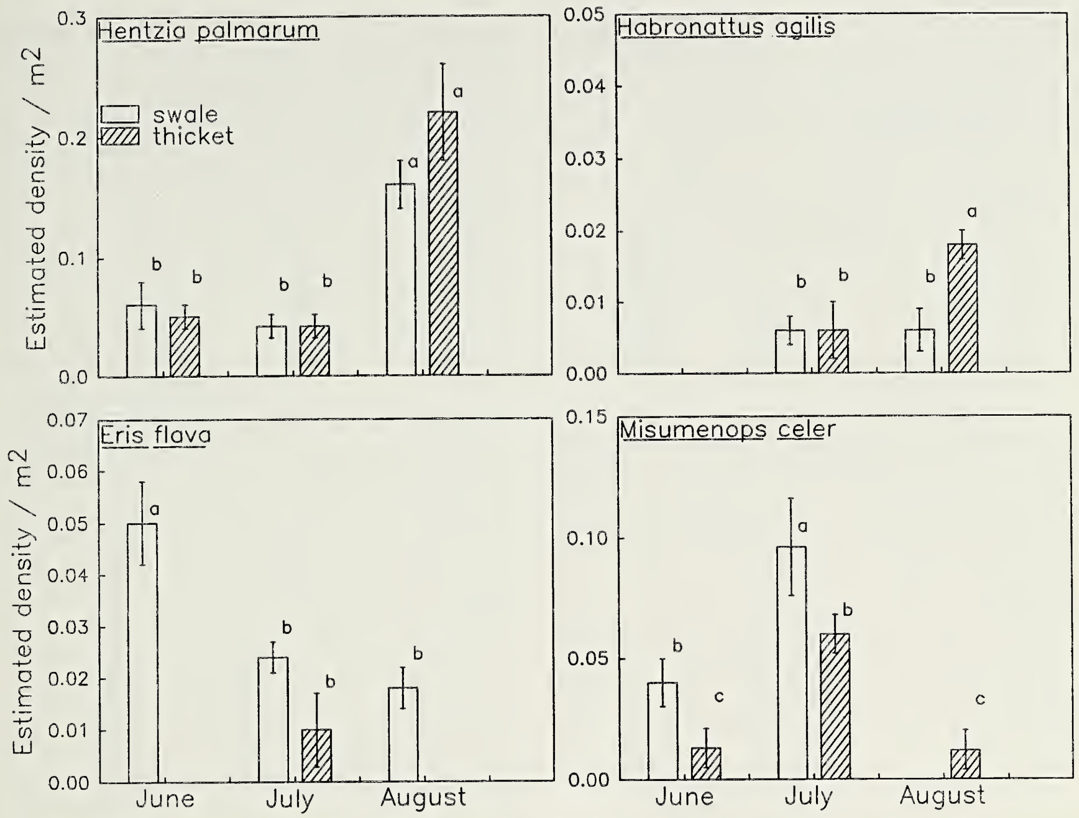

Figure 3.—Estimated densities of the four primary species composing the spider guild on *Myrica cerifera* in June, July and August of 1995. Vertical bars indicate one standard error of the mean. Letters indicate significant differences ($P < 0.05$) in density between site.

Most insects were identified using field guides (Borror & White 1970; Helfer 1987). Ants were identified by Deborah Waller at Old Dominion University. Voucher specimens of the spiders are located at the University of Kansas.

Four sweepnet samples were taken at each of the four study sites along linear transects running parallel to the dune ridge. These 16 samples were equally divided between the developing thicket and the early transitional swale and included sweeps of 100 *Myrica* or *Baccharis* plants in either habitat (Fig. 2). This 16 sample collection procedure was repeated in early June, July and August, 1995. Density of *Myrica* and *Baccharis* shrubs at both study sites were counted using 15 quadrats, each five m^2, delineated with corner posts and a tape measure. The estimated density of spiders and prey was then determined by multiplying the number of individuals per plant (total n/100) by the density of plants/m^2. This method gives an estimate of spider and prey insect density/m^2.

Two samples (50 sweeps/sample) were also taken in the graminoid dominated areas of the colonizing swale around individual *Myrica* and *Baccharis* plants in June, July and August. These additional samples were taken to survey spider and insect species diversity in swales and to qualify any overlap of species between swale graminoids and shrubs.

Data for spider and insect density changes with season were analyzed by 2-way ANOVA (site × season) in SAS using an $\alpha = 0.5$ (Zar 1984; SAS Institute 1988).

RESULTS AND DISCUSSION

Density of spiders on both shrubs was highest in August. This increase from the previous two measurement periods was primarily due because of the increase in density of *Hentzia palmarum* (Araneae, Salticidae) (Figs. 3, 4). There were no differences in density in *Hen-*

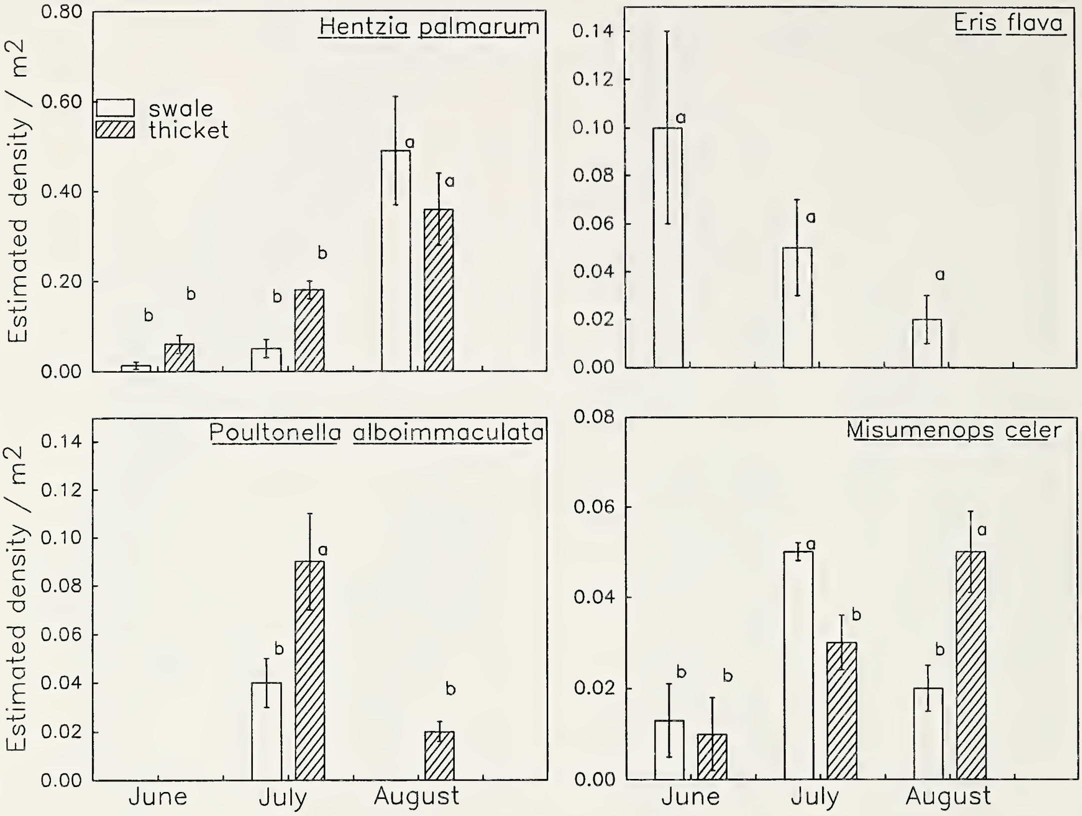

Figure 4.—Estimated densities of the four primary species of the spider guild on *Baccharis halmifolia* in June, July, and August. Vertical bars indicate one standard error of the mean. Letters indicate significant ($P < 0.05$) differences in density between sites.

tzia palmarum on *Myrica* between habitats. On *Baccharis*, *H. palmarum* was more common in the developing thicket but was more evenly divided between habitats in August. Similarly to *H. palmarum*, *Habronattus agilis* (Araneae, Salticidae), also showed significantly ($P < 0.05$) higher densities in August. It was only found on *Myrica* and was most frequently captured in the developing thicket (Fig. 3).

Misumenops celer (Araneae, Thomisidae) had the highest density of individuals on both *Myrica* and *Baccharis* in July. On *Myrica*, *Misumenops celer* had significantly ($P <$ 0.05) higher density in the early transitional swale. This pattern was also evident for *Baccharis*; however, there was no significant difference in density between the sites. Also on *Baccharis*, *M. celer* had significantly ($P <$ 0.05) higher density in plants of the developing thicket (Fig. 4).

Eris flava (Araneae, Salticidae) was also found on both *Myrica* and *Baccharis* but was primarily found in the early transitional swale site. While it was found on *Myrica* in the developing thicket, it was never found there on *Baccharis*. The changes in density of *E. flava* from June to significantly ($P < 0.05$) lower densities in July and August show a trend opposite to that found for *Hentzia palmarum* and perhaps also *Habronattus agilis*.

Eris flava may have been more common on *Myrica* and *Baccharis* plants in the early transitional swale because it was a prominent member of the surrounding graminoid community. In these areas, *E. flava* was found in a density of 21 individuals/100 sweeps in June, 30/100 sweeps in July and 45/100 sweeps in August. These numbers are not expressed as a density/m^2 because an intensive study of the swales was beyond the scope of this study. Nevertheless, the apparent increase in estimated density suggests a trend opposite to that found on *Myrica* and *Baccharis* over

the measurement period. *Eris flava* may have been responding to a rapid increase in juvenile planthoppers (unidentified) which were found in density of 62 individuals/100 sweeps among graminoids in August. Other spiders of the graminoid dominated swale community were, in order of highest to lowest density, *Mangora gibberosa* (Hentz 1847) (Araneae, Araneidae), *Tetragnatha versicolor* Walckenaer 1981 (Araneae, Araneidae), *Marpissa pikei* (G.& E. Peckham 1888) (Araneae, Salticidae) and *Tibellus oblongus* (Walckenaer 1802) (Araneae, Philodromidae).

Another prominent component of the spider community on *Baccharis* was *Poultonella alboimmaculata* (Araneae, Salticidae). Like *M. celer*, *P. alboimmaculata* had the highest estimated density on *Baccharis* in July; however, it was not found in June and was found in very low numbers in August (Fig. 4). This species has been found in the upper midwest and on the east coast in New York State but has not been previously observed on the Virginia barrier islands (Cokendolpher & Horner 1978; Steitenroth & Horner 1987). Therefore, this may represent a new southeastern record for the species (J. C. Cokendolpher & B. Cutler, pers. comm.). These *P. alboimmacultata* were also found most commonly associated with the ants, *Forelius pruinosus* (Roger) in the early transitional swale and with *Crematogaster clara* Mayr in the developing thicket. While *Dolichoderus mariae* Forel was as common on *Baccharis* as *Crematogaster clara*, *P. alboimmaculata* was never found associated with that species.

The most common insect on *Myrica* at both sites was the tree cricket *Oecanthus fultoni* T. J. Walker (Orthoptera, Gryllidae, Oecanthinae). *Oecanthus* was found in high density in June and July. The density of *O. fultoni* was significantly ($P < 0.05$) lower in August (Table 1). *Oecanthus fultoni* was also found on *Baccharis* but occurred there only sporadically and in minimal numbers. The most common insects on *Baccharis* were *Trirhabda bacarhidis* (Chysomelidae), aphids (unidentified) and five species of aphid-tending ants. Among the ants, *Dolichoderus mariae* Forel, *Crematogaster clara* Mayr and *Forelius pruinosus* (Roger) were the most common. Further description of the ant communities was beyond the scope of this study.

Table 1.—Estimated densities of *Oecanthus fultoni* Walker on *Myrica cerifera* at the colonizing swale and developing thicket sites. Numbers represent the mean ± one standard error. Letters (a, b) indicate significant ($P < 0.05$) differences in density.

	Developing thicket	Colonizing swale
June	5.1 ± 2.3^a	3.4 ± 1.6^a
July	8.6 ± 3.3^a	3.7 ± 2.0^a
August	0.3 ± 0.12^b	0.4 ± 0.17^b

In conclusion, the spider communities associated with *Myrica* and *Baccharis* are very similar in species diversity but chiefly differ in density with *Baccharis* supporting fewer individuals. Both shrubs growing in the early transitional swale share one species, *Eris flava,* with the surrounding swale community. Generally spider diversity and density differed most between sites rather than between shrub species. Though species were generally identical for both shrubs, the rare jumping spider *Poultonella alboimmaculata* was only found on *Baccharis*.

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HABITAT AND COURTSHIP BEHAVIOR OF THE WOLF SPIDER *SCHIZOCOSA RETRORSA* (BANKS) (ARANEAE, LYCOSIDAE)

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ABSTRACT. The habitat and courtship behavior of the wolf spider *Schizocosa retrorsa* (Banks 1911) were studied and are described here for the first time. The range of *S. retrorsa* was extended to include the lower peninsula of Michigan. This species is locally abundant in highly exposed habitats of sand or pine litter. Male courtship consists of chemoexploration, palpal drumming, an extended leg tap, and a "push-up" display. Female displays include a double leg arch, approaches, and orientations toward the male.

Courtship behavior in spiders has been of interest to arachnologists for some time and continues to be a common area of study (Peckham & Peckham 1889; Kaston 1936; Rovner 1968; Stratton 1985). The visual signals of the brightly colored Salticidae and the large Lycosidae have probably made them particularly conspicuous to human researchers. Along with the rather conspicuous visual signals, lycosids have also been shown to use acoustical or vibrational communication through the use of a palpal stridulatory organ (Rovner 1975). The importance of chemical communication has also been investigated (Tietjen 1977, 1979). However, the relative importance of visual, chemical, tactile, and acoustical or vibrational communication in any one species or habitat has only recently been addressed (Scheffer et al. in press).

Some of the most comprehensive studies of spider courtship have been conducted with species within the wolf spider genus *Schizocosa* (Kaston 1936; Montgomery 1903; Hegdekar & Dondale 1969; Uetz & Denterlein 1979; Stratton & Uetz 1981, 1983; Rovner 1973; Stratton 1982; and Stratton & Lowrie 1984). Courtship behavior has been described for a handful of *Schizocosa* species, primarily in the *S. ocreata* species group. The role of male courtship behavior as a reproductive isolating mechanism has proven to be very important in at least two species. *Schizocosa ocreata* (Hentz 1844) and *S. rovneri* Uetz & Dondale 1979 are reproductively isolated due to their courtship behavior (Stratton & Uetz 1981, 1983, 1986; Uetz & Denterlein 1979; Stratton, Miller, & Hebets unpubl. data). When forcibly mated, interspecies hybrid offspring are also reproductively isolated by behavior (Stratton & Uetz 1986). *Schizocosa ocreata* and *S. rovneri* are thus termed "ethospecies", i.e., species reproductively isolated by behavioral mechanisms of courtship (Hollander & Dijkstra 1974). The acoustical components of *Schizocosa* courtship are crucial to the reproductive isolation of these ethospecies. It has been suggested that this acoustical variation may, in part, be due to habitat differentiation (Stratton & Uetz 1986).

Schizocosa retrorsa (Banks 1911) is widespread and is known from 38 collections from the midwestern and eastern United States (Dondale & Redner 1978). Although Dondale & Redner (1978) offer a description of this species, little is known of its ecology and behavior.

Here we provide an analysis of the male and female courtship behaviors of *Schizocosa retrorsa* and discuss the possible impact of the habitat of this species. The behavior of *S. retrorsa* is of interest because it is not a member of the *S. ocreata* species group. *Schizocosa*

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retrorsa occurs in a different habitat from the *S. ocreata* group, and the male secondary sexual characteristics (seen as black brushes of hair on the male forelegs, pigmentation on male forelegs, etc.) are different from those species previously studied.

METHODS

Specimens.—Penultimate and mature males and females were collected at night from five sites in Lafayette, Marshall, and Panola Counties, Mississippi and one site in Berry County, Michigan between 15 June–29 June 1993. Collection sites were **MISSISSIPPI**: *Lafayette County* --University of Mississippi campus, Old Taylor Road near baseball stadium T8S R3W Sect. 29, 34°21′N 89°32′30″W; and 8 mi. SE Oxford T10S R3W Sect. 35, 34°36′N 82″29′W. *Marshall County* --3.8 mi. N of N end of Tallahatchie Bridge on Old Highway 7. T6S R3W Sect. 2, 34°36′N 89°29′W; and 1 mi. N of Wall Doxey St. Park on pipeline E of Hwy 7. T5S R3W Sect. 1, 34°40′N 89°28′W. *Panola County* --near Sardis Dam. T8S R6W Sect. 13, 34°23′N 89°47′30″W. **MICHIGAN**: *Berry County* --Deep Lake Campground, Yankee Springs Recreation Area. Specimens from this study are housed at the University of Mississippi. Voucher specimens are deposited in the Mississippi Entomological Museum at Mississippi State University.

The spiders were transported to the laboratory and held individually in 8 cm × 4 cm plastic cages in a controlled environment (21 °C and 12L:12D cycle). Water was provided via a cotton wick dipped into a reservoir below the cage. Spiders were fed several small crickets approximately twice each week.

Behavioral observations.—Between 23 June–15 July 1993, we videotaped interactions of 23 pairs of mature males and females (all of which were between 8–23 days post maturation molt). Females were removed from their cages approximately 12 hours before a pairing and were placed on filter paper in culture dishes. Prior to recording, the female and filter paper were transferred to a 9.5 cm transparent cylindrical observation arena. The filter paper was positioned in such a way that approximately 0.5 cm of it extended beyond the wall through a slit at the bottom of the cylindrical arena. A sound transducer (stereo needle) was placed on the protruding edge of the paper. The female was constrained within a 4 cm transparent barrier inside the observation arena that could be removed when appropriate. The male was gently introduced into the arena through a 20 cm long 1.5 cm diameter glass tube.

Video recordings were made with a Panasonic HD-5000 video camera with either a 105 mm macro (1:1, f/2.8) lens for close-up recording of the male or a 10.5–125 mm zoom (1:16, 12×) for sequences involving both the male and female. Stridulatory sounds were recorded from the substratum with a stereo needle transducer attached to an EG & G PARC, Model 113, preamp (Gain set at 5K, low roll off set at 0.3Hz, high roll off at 10kHz) and overlaid onto the videotape.

Video and acoustic recording began when the male was introduced and continued for approximately 10 min. If no courtship was seen, the male was scored as "negative" and was replaced. If a male showed courtship display, the females were watched closely for signs of receptivity (e.g., jerky walk, pivots, orientation toward the male). If a female seemed to be receptive, the barrier was lifted and the male and female were allowed to interact.

Seven copulations were observed. When copulation occurred, it was videotaped for 10–45 min. Total times of copulation were recorded for two of the pairings. Most of the copulations were recorded on videotape for only a short period of time, after which the pair was removed from the camera's field of view (these spiders were allowed to continue copulating). After each pairing, the observation arena was swabbed with alcohol.

Analysis of behavior.—Of 23 male-female pairings, 20 were scored (three tapes could not be scored due to camera angles). The pairings were first separated into four categories: pairings that ended in copulation (n = 7), pairs with males that courted but did not copulate (n = 5), pairs that neither courted nor copulated (n = 5), and pairings in which the female was aggressive towards the male (n= 3).

A one minute video sequence for each pairing was scored for sequences of actions, repetition of behaviors, intervals between behaviors, duration of behaviors and, when feasible, positions of both males and females. For the pairs that copulated, the scored minute was that minute directly preceding the mount by the male. Males will begin their courtship

when simply introduced to a female pheromone and do not necessarily immediately orient to a female when one is present; thus courtship or orientation cues did not provide good starting points for analysis of behavior. For the pairs that did not copulate, the scored minute was a segment of tape which included a courting male and a female after removal of the barrier. No criteria were used for choosing the scored minutes of non-courting pairs. The scored minute for the pairings with the aggressive females directly preceded a "lunge" towards the male by the female.

The six behaviors that we examined closely in comparing these courtship displays were: male "push-ups", male extended leg taps, female double leg arches, female approaches, female orientations, and male orientations. Instances in which the males displayed a "defensive stance" when confronted with an unreceptive female were also noted.

Statistical analysis.—Two tailed *t*-tests were done on the frequencies of male extended leg taps, male "push-up" displays, and female double leg arches to compare the frequencies between pairs that copulated and pairs that only courted.

RESULTS

Habitat.—The first Lafayette County, Mississippi site was a mowed sandy hillside adjacent to a major road; a second site was in an open pine woods (Lafayette County); third and fourth sites were exposed "borrow pits" which were sandy with lichens (Marshall County & Panola County); and a fifth site was a sandy grassy pipeline along the highway (Lafayette County). The Berry County, Michigan site was an open sandy field.

Description of courtship.—The male courtship consists of four basic displays: (1) chemoexploration, (2) palpal drumming, (3) extended leg tap, and (4) "push-up".

In the pre-courtship display (the "searching phase"), males walk around the arena until they come into contact with female silk, after which the male exhibits chemoexploration (Stratton & Uetz 1983). In chemoexploration, males move the palps by rubbing the dorsum of the palp against the substratum in a circular motion as described by Tietjen (1979). The display typically lasts only a few seconds. The behavior is used presumably for detecting pheromones that may have been left by a female and takes place almost immediately when a male is introduced to female silk.

Chemoexploration was typically followed by palpal drumming (1–3 drums/sec). In this behavior, the male quickly lifts and lowers his palps as if they were beating on a drum. There is sound produced during this display, but we cannot state whether the sound is made strictly from the drumming or from stridulatory organs located in the palps. The male stands motionless during palpal drumming with the long axis of the body parallel with the substratum. Bouts of palpal drumming are interspersed with rest periods. Palpal drumming takes place even when a female is not physically present.

As palpal drumming continues, the male displays an extended leg tap. In this display, the right or left leg I is lifted, extended, lowered, and then tapped on the substratum at a rate of several taps per second. Each tap brings the leg nearly perpendicular with the substratum. It is not clear if the leg comes in contact with the substratum or not. There is sound accompanying the extended leg tap, but the sound has not been verified as to be coming from the palps (tapping or stridulation) or from contact of leg I on the substratum. The extended leg tap gives a strobe effect due to the contrast between the black femur of the foreleg and the white of the tibia.

The fourth display in the male's courtship is the "push-up" behavior. This behavior is given when the male turns to orient towards a female or when he is resuming his palpal drumming after a pause. During the push-up display, the male begins with his body lowered to the substratum and displays palpal drumming. He lifts his entire body up onto the tips of his legs. During the lifting of the male's body, a loud stridulation, almost a click, is audible. It is not obvious how the clicking noise is made.

We identified two distinct female behaviors: (1) double leg arch, and (2) approach. In the double leg arch, the female lifts legs I and II on either her right or left side. As the legs are lifted into the air, the femurs are nearly perpendicular to the long axis of the body carapace and the bending ("arching") occurs at the femur-patella joint and the tibia-metatarsus joint; the femur, tibia, and tarsus form three sides of a square.

Females of *S. retrorsa* also display an ap-

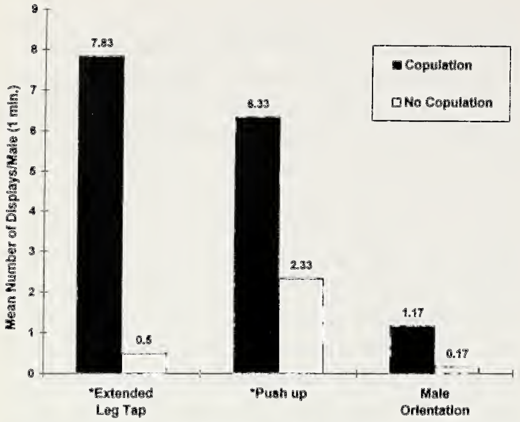

Figure 1.—Comparison of the frequency of three male courtship displays between pairings that ended in copulation and pairs in which the male courted but no copulation occurred. (★) indicates that there is a significant difference between pairings that copulated and those that did not.

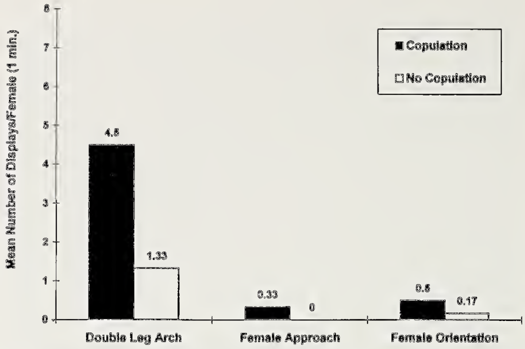

Figure 2.—Comparison of the frequency of three female courtship displays between pairings that ended in copulation and pairs in which the male courted but no copulation occurred.

proach behavior. A receptive female will approach a stationary, courting male either from the side or from the back. The approach is very slow and seemingly deliberate, often with double leg lifts intermittently displayed. On a few occasions, the female turns and orients herself directly in front of a courting male, placing herself in what is apparently a pre-mounting position.

The mount of the male onto the female is very rapid; there is no grappling. During copulation, the male inserts a palp several times on each side (seen in all seven pairs that copulated) with disengagement of the palp after each hematodochal expansion. This is followed by a switching to the opposite side, where there are once again multiple insertions. The female rotates her abdomen laterally so that the male genital bulb can come into contact with her epigynum.

Analysis of behavior.—The spider pairings that ended in copulation showed a significantly higher number of extended leg taps ($t = 3.62$, $df = 9$, $P < 0.05$) by the male than pairs that courted but did not copulate (Fig. 1). The number of push-up displays by the male between these two pairings was also calculated to be significantly different ($t = 2.29$, $df = 9$, $P < 0.05$).

The mean number of double leg arches by the female appears much larger in pairs that copulated (Fig. 2) but there was no statistical difference ($t = 1.02$, $df = 9$, $P < 0.05$). The double leg arch was also observed in aggressive females.

Neither push-up displays, leg taps, nor orientations by either sex were seen in the non-courting pairs nor when the females were aggressive. Both male and female orientations toward the opposite sex were seen most frequently in pairings that ended in copulation (Figs. 1, 2). The latency to copulation of the pairs mated in the laboratory ranged from 5 min, 13 sec (00:05:13 min) to 1 h, 18 min, 1 sec (01:18:01 min). A flow chart showing the frequency of different sequences of male and female displays gives a visual image of the patterns of behavior that occur in both sexes throughout the courtship display (Fig. 3).

Copulations and egg sacs.—In 17 of 23 pairings, males showed courtship displays (74%). Seven of these courtship displays ended in copulation and three of the mated females produced egg sacs. In three pairings, the female was aggressive; and in two of these cases, the males were killed by the female.

Copulations were observed in the laboratory during the period of 23 June–8 July, covering a two-week time span. Two copulations, excluding any courtship, were timed with the first lasting 2 h, 30 min (02:30:00 min) and the second lasting 2 h, 40 min (02:40:00 min). The three females mated in the laboratory produced their egg sacs 25, 28, and 40 days, respectively, after copulation ($\bar{X} = 31$ days, $SD = 7.9$).

Seventeen of the females that were mature upon collection, but not used in any laboratory trials, produced egg sacs. For these females, the time from their collection to egg

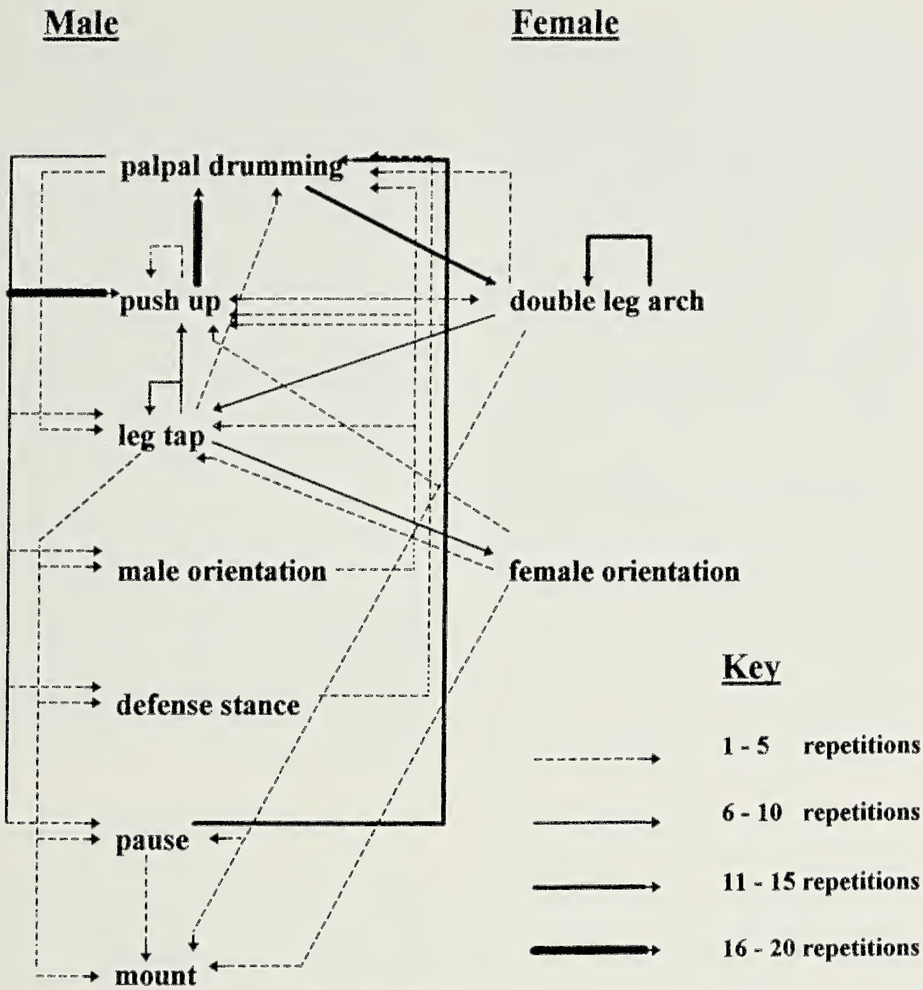

Figure 3.—Flow chart of male and female *Schizocosa retrorsa* courtship displays.

sac production ranged from 21–63 days ($\bar{X}$ = 33 days, SD = 10.4).

Four of the 17 females produced a second egg sac after having lost their first. The second egg sacs were produced between 24–30 days after the first sac was dropped ($\bar{X}$ = 25.5 days, SD = 3.5). Most of the egg sacs were abandoned by the females during shipment from Mississippi to Michigan in the middle of August 1993. Two females successfully hatched young 42–45 days respectively after egg sac production.

DISCUSSION

Habitat.—Species of *Schizocosa retrorsa* tend to be found in highly exposed areas in the presence of sand or pine needles. It is possible that sand and pine needles play some role in camouflaging the spider, thus aiding in their protection. The light sandy color of the legs would seem to blend in quite well with sandy ground or dead pine needles. The broken bands along the carapace, seen as dots, could also aid in this blending. Although the entire body of the female is a light sandy color, the male possesses very distinct black pigmentation on his femur of legs I. This femur not only greatly contrasts with the sandy color of the ground, but it also contrasts with the light color of the male's tibia. This distinct contrast on the forelegs of the male, we believe, aids in his attempt to attract the attention of a female. As male spiders spend most of their lives as immatures with the same camouflaged coloration as females, this pigmentation may be linked to courtship as it is only

upon reaching sexual maturity that they no longer blend in with the environment.

It is apparent that sound as well as vision constitutes a large portion of courtship for this particular species. Many members of the genus *Schizocosa* stridulate, yet few show palpal drumming (*S. mccooki* (Montgomery 1904) shows "bursts" of percussion; Stratton & Lowrie 1984). It is possible that the substratum upon which these species are found is the best conductor for their particular courtship sounds. Sand or pine needles may transmit the acoustical signals most effectively for *S. retrorsa*. Further work is needed to test this hypothesis.

Courtship.—Much of what is known of the courtship rituals of different species within the genus *Schizocosa* suggests that courtship tends to deal a significant amount with the foreleg patterns of the male spider. Since the mature males of *S. retrorsa* have black pigmentation on the femur of their forelegs, it is not surprising that this generalization holds true for this species also.

The extended foreleg tap of the male is apparently a key display in the success of his courtship. In two instances (Fig. 3) the leg tap directly preceded a successful mount by the male. This extended leg tap is a striking display that is presumably very conspicuous to female spiders. The significantly larger number of extended leg taps displayed by males that eventually copulated supports the notion that this display is of great importance in the success of male *S. retrorsa* courtship. Once again, further research is needed to pinpoint exactly what it is about this behavior (vigor, intensity, frequency, etc.) that makes males more or less successful.

Although the male push-up display is apparently important in courtship, it does not seem as tightly linked to copulation as is the extended leg tap. The push-up display seems to be a starting point for males; it normally follows a long pause or a male walk or turn. Since the push-up display was seen only in males that courted and in every courting male except one, it is apparently an integral part of male courtship. There may be a certain ratio between extended leg taps and push-up displays that is most effective for courting males.

The female displays are a bit more difficult to interpret. The female orientation and approach seem to be clearly linked to copulation. The approach by a female was only observed in pairs that copulated and female orientations were observed only in the presence of a courting male. However, the female double leg arch is seen not only in the presence of courting males, but it was also displayed by aggressive females. Using the term "female courtship" for the female double leg arch display may not be very accurate. Perhaps unreceptive females are engaging in this "receptive" behavior in order to entice a male to approach and thus ensure a meal.

Copulation.—The relatively long duration of copulation (2–3 h) in *Schizocosa retrorsa* is similar to that in other members of the genus. These spiders may incur a higher risk of predation by engaging in copulation for several hours on the forest floor; there must be a benefit for this long copulation (e.g., fertilization, etc.), but it is yet unknown.

The pattern of palpal insertion during copulation for *S. retrorsa* is also similar to that in other members of the genus in that there are several insertions per side with palpal disengagement between hematodochal expansions (Rovner 1973).

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DIFFERENTIAL MORTALITY AND RELATIVE MATERNAL INVESTMENT IN DIFFERENT LIFE STAGES IN *STEGODYPHUS LINEATUS* (ARANEAE, ERESIDAE)

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ABSTRACT. The general reproductive pattern in spiders is to produce large clutches with small eggs although some species produce a few, large eggs. The spider *Stegodyphus lineatus* (Eresidae) is unusual in that it lays a single extremely small clutch and has small eggs. The female feeds the young after hatching and eventually the young completely consume her.

Differential mortality risks in different life stages may provide an explanation of relative maternal investment in eggs *versus* hatchlings. By monitoring natural populations of *S. lineatus*, sources and rates of mortality were assessed during the reproductive period. Complete failure of reproduction was more likely during egg development than after the spiderlings had hatched. This was partially explained by the presence of a parasitoid wasp that only attacked females before the young had hatched. Overall attack rates were similiar in the egg stage and in the hatchling stage; however, the spiderlings suffered less mortality because they were mobile.

By allocating the major reproductive effort to hatchlings rather than eggs, these spiders may pass through the risky egg stage relatively fast; and overall development and growth can be maximized. Small egg size might be an adaptation to high predation pressure during the reproductive period. Small clutch size can be explained by the importance of early growth for offspring fitness.

Parental care is considered to increase the survival probability, and often the reproductive value, of offspring (Clutton-Brock 1991). Accordingly, parental care is usually associated with a high investment per individual young (Shine 1978; Sargent et al. 1987; Stearns 1992). Assuming that a female has a limited amount of energy to invest in reproduction, an increase in investment per individual young will reduce the number of offspring that can be produced. Thus one may expect that animals with brood care will have relatively few but large offspring. This is indeed the case in many oviparous ectotherms, where the amount of parental care and propagule size are positively correlated (Shine 1978; Gross & Sargent 1985; Sargent et al. 1987; Clutton-Brock 1991; Roff 1992).

Large propagules can be achieved in two different ways: resources can be invested in offspring either by providing them with yolk at the egg stage or enhancing growth by feeding the young after hatching. The first form of resource allocation is the more common one in oviparous ectotherms in which parental care is mostly egg guarding and is associated with relatively large eggs (Shine 1978). However, extended brood care does occur in many species; and differences in the allocation of resources into the various developmental phases may be a result of different predation pressures in the different stages, with selection pressures similar to those proposed for the evolution of egg size *per se* (Shine 1978, Sargent et al. 1987). In the "safe-harbor" hypothesis, Shine (1978) proposed that in oviparous ectotherms that large eggs should evolve if predation pressure is high during the juvenile stage, and small eggs should be selected for if mortality is relatively high in the egg stage.

In many species, total clutch mass is a function of female body mass (Craig 1987; Anderson 1990; Marshall & Gittleman 1994). Variation in clutch mass mostly results from differences in clutch size rather than in egg size (Marshall & Gittleman 1994). Most spiders lay several large clutches with small eggs

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and die before the young hatch (Foelix 1981; Marshall & Gittleman 1994). The parental care they exhibit is to spin silken cocoons around the eggs and to position these cocoons in places where access for predators is difficult. Some spiders guard their egg sacs and may carry their young after hatching. After correcting for female body size, Simpson (1995) found no difference in clutch size nor in egg size between spider genera that guard eggs and carry young and those genera that provide less or no parental care. Simpson (1995) concluded that female size, and not the type of parental care, is the primary factor that influences clutch and egg size in spiders. Extended maternal care that includes the feeding of young is less common in spiders and has not been included in comparative studies of egg and clutch size.

The eresid spider, *Stegodyphus lineatus* Latreille 1817, is unusual in that females produce small clutches with small eggs and also exhibit extended maternal care. The average clutch mass represents only 2–3% of the female's body mass which is an extraordinarily small investment in eggs (see Marshall & Gittleman 1994, the smallest female mass/clutch mass ratio in a sample of 40 species is 16%). Other spider species of a similar body mass of 200–500 mg lay several hundreds of eggs (Marshall & Gittleman 1994); *S. lineatus* lays only about 70. Instead, *S. lineatus* females invest all their remaining resources into the spiderlings after they hatch. Females release the spiderlings from the egg sac and feed them via regurgitation. The young consume their mother's entire body content, and she dies about two weeks after the young hatch. Consequently, juveniles disperse at a relatively large size. Similar forms of maternal care, involving provision of food for the young, have evolved in at least six spider families: Agelenidae, Amaurobidae, Eresidae, Heteropodidae, Theridiidae, Thomisidae (Kullmann & Zimmermann 1974; Gunderman et al. 1988; Tahiri et al. 1989; Henschel 1990, Evans et al. 1995).

Although Shine (1978) and Sargent et al. (1987) do not explicitly consider the case of extended parental care, their ideas may be applicable to it. Thus, the "safe-harbor" hypothesis (Shine 1978) would predict that the strategy of extended brood care and small egg size may be adaptive if predation pressure is higher in the egg stage than in the hatchling stage. Testing the "safe harbor" hypothesis requires a comparative approach; however, qualitative predictions derived from this theoretical framework can be applied to a single species to ask whether differential predation pressure is at all likely to be an explanation for the unusual resource allocation by the desert spider *Stegodyphus lineatus*. Predation pressure would not be a likely explanation for small egg size if the hatchling stage is at greater risk than the egg stage. A natural population of *S. lineatus* was monitored over their entire reproductive season in order to assess risks and causes of mortality during different reproductive stages. I attempted to determine whether predation pressure differs for the egg stage and the hatchling stage.

METHODS

Study animals.—*Stegodyphus lineatus*, a sedentary spider, builds a retreat in the form of a silk tube; and the web radiates from the entrance of the tube to the nearby vegetation. The size and form of the web depends on vegetation structure and the size of the spider (Ward & Lubin 1993). The average body length of adult females at egg laying in the Negev population was 13.42 mm (SD = 1.44, n = 278). Each female produces a single clutch, and will produce a second clutch only if the first is lost. Egg number is a function of female body mass and varies between 40–140 (mean = 70, n = 53) eggs per clutch. This study started at the end of the mating season when some males were still wandering around in search of mates or cohabiting with females. Voucher specimen of the species are in the National Collection of Israel.

Study site.—The study site was a wadi (dry riverbed) of about 3 km length located on the Avdat plateau, Negev Desert, Israel. The wadi was in a Bedouin grazing area; and goats, sheep, donkeys, and camels foraged in the area every day. Spider densities were higher in the wadi bed than on the slopes. Webs were patchily distributed on shrubs or dry annual vegetation with densities up to 20 webs per 25 m^2.

Monitoring.—During the first half of May 1993, I marked the nests of 327 female *S. lineatus*. It was not possible to find and mark all spider nests that occurred in the wadi during the first days, and several were over-

looked. These nests were marked on the day first encountered and were included in the sample from then on. Adult females usually do not leave their nests, and females with eggs or young never do so. Only 12 times did I find a female with a new tube. It is possible to distinguish old from new webs by the size of the tube and the occurrence of plant material incorporated in the silk. As a consequence of the continued marking of some webs, sample sizes changed during the observation period. Therefore, daily survival rates were calculated relative to the number of spiders on the previous day. Mortality at day "*x*" was expressed as the percentage of dead spiders relative to the number of spiders at day "*x − 1*". Daily survival probabilities were calculated by *1 − (mortality/100)*. Daily probabilities were multiplied to obtain the cumulative survival probability function.

Definitions of developmental stages in spiders vary considerably in the literature. I will refer to the egg developmental period as the time from laying until hatching from the cocoon. The hatchling period starts when the young leave the egg sac and ends at the day they start to disperse. The survival probabilities in the egg period and the hatchling period were calculated relative to the total number of females with eggs (n = 278) or young (n = 127), respectively. The day of egg laying or hatching was set as Day 1 in each case.

Each tube was checked daily at dawn. I recorded whether the females had egg sacs or hatched spiderlings. I also documented whether females had died or disappeared and, if known, the cause of death. The four main predators can be identified by indirect or direct methods. The parasitic wasp *Pseudopompilus humboldti* Dahlbom 1845 deposits an egg on the abdomen of the adult female spider and leaves the spider in the entrance of the nest (Ward & Henschel 1992). The main spider predator, *Poecilochroa senilis* O.P.-Cambridge 1872 (Gnaphosidae), usually stays in the nest feeding on the host for several days. Ant attacks could often be observed or they were identified by the large number of dead ants in the web, and bird or rodent predation always resulted in removal of the whole nest. The same data were recorded to quantify mortality of egg sacs or spiderlings. I never found any evidence for egg sacs being parasitized. Each time an egg sac hatched, measurements

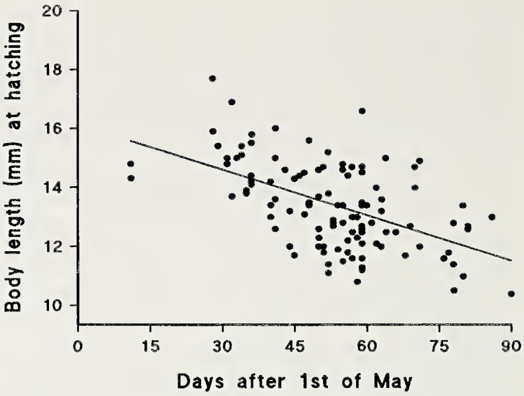

Figure 1.—Relation of female size (body length in mm) at hatching of young and the hatching date, given in number of days after the first day of May.

of the female's body length, prosoma width and opisthosoma width were taken and the number of hatched spiderlings was estimated as exactly as possible without having to destroy the nest. Spiderlings were counted again 25 days after they had emerged from the egg sac. Spiders were measured in an acrylic plastic ("Plexiglas") tube covered on one end with translucent plastic wrap. The spider was fixed against the plastic wrap with an additional inner tube covered with soft foam-rubber. Using a pair of calipers, body parameters were measured to the closest 0.1 mm with an error of 0.2 mm (maximal 5%), estimated from repeated measurements.

RESULTS

At the beginning of the study period (2 May 1993) 2% of 327 females had already laid eggs. The relative number of females with eggs increased every day, and after four weeks 80% of all marked females had reproduced. Some spiders did not reproduce. The average duration of egg development was 30 days (SD = 4, n = 108). Early reproducing females were larger than females that laid eggs later in the season ($r^2 = 0.27$, $P < 0.001$, $y = -0.05x + 16.14$) (Fig. 1).

The survival function of all adult females regardless of their reproductive state (in the study area over a period of three months) is shown in Fig. 2. Daily survival rates were similar throughout the reproductive season. Thus, the faster a female can complete reproduction, the lower her risk of dying from pre-

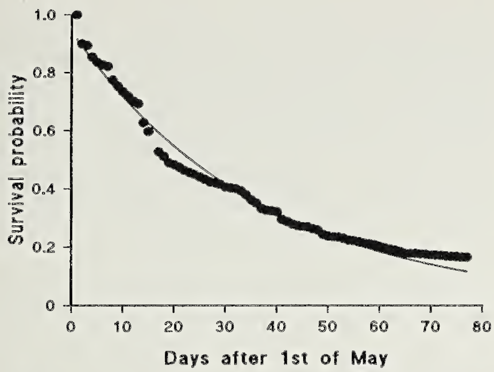

Figure 2.—Cumulative probability of survival of the Negev population over the reproductive period lasting from the first day of May to middle of July; curve fit: A * $e^{(-k * x)}$, A = 0.94, k = 0.027; r^2 = 0.98.

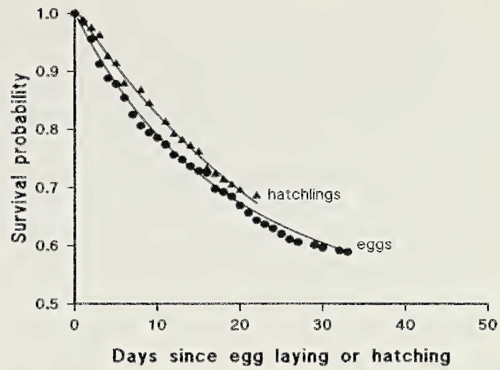

Figure 3.—Comparison of the survival probability during the egg period (circles) and the hatchling period (triangles). Both curves are fitted by the same log logistic functions: A −ln (1 + B * $e^{(-k * x)}$, for the egg period (r^2 = 0.996), k = 0.043, B = −0.401, A = 0.488; and for hatchling period (r^2 = 0.995), k = 0.019, B = −0.543, A = 0.227.

dation. However, the curve is flatter at the end when many broods have hatched.

Rates and causes of mortality during the egg development period.—Since reproduction was not synchronous, the day of egg laying was set as Day 1 (Fig. 3) in order to compare the survival of females in different states of reproduction. The figure shows only the mortality of females, not the eggs, because the young depend completely on their mother whereas females can re-lay if they lose a clutch. Of 278 females which produced first egg sacs, 63 lost them, mainly due to predation of egg sacs by ants or males of *S. lineatus* (unpubl. data). Nine females lost their first and second clutch, two lost three clutches and one lost four. Overall, 63 females lost 79 egg sacs. If a spider lost her first clutch, she lost, on average, 20 days (SD = 7.5, n = 59) which is the sum of the mean age of the lost eggs plus the mean of 11.6 days (SD = 4.4, n = 59) that it took to produce a replacement clutch. This time loss corresponds to a decrease in survival probability of about 15% (Fig. 2). Eight females died before they could produce a second clutch. Fifty-five females laid a replacement clutch but only 16 survived until their young hatched.

Of 278 females with egg sacs, 145 (52.16%) died during the development of their eggs and an additional six never produced an egg sac that hatched. If the female died but the egg sac stayed intact, she still had no reproductive success because spiderlings are not able to leave the egg sac without the help of the mother. In total 169 females (61%) were attacked by predators at least once during the egg development stage. Sixty-three lost only their eggs and had another chance to reproduce. Some of these females were attacked again with lethal consequences: 59 females were attacked at least twice. In total, 224 predator attacks were counted.

Largely due to predation during the period of egg development, 54.3% (145 dead + 6 unsuccessful) of all females had no reproductive success. The parasitic wasp *Pseudopompilus humboldtii* parasitized 39 females (i.e., 14% of the population of females with eggs). Other predators were birds (n = 32, 11.5%), ants (n = 16, 5.7%) and spiders (Gnaphosidae) (n = 10, 3.6%). The predator was not identified in 48 (17.3%) of the cases of female mortality. In total, 127 (45.7%) females survived until their young hatched.

Mortality during the hatchling period.—Young hatched from clutches of 127 females. Of these, 88 broods (69.3%), with an average of 13.1 (SD = 7.9) dispersing young, survived until the young reached an age of 25 days. Predators attacked 64% (n = 81) of all broods; however, only 48% (n = 39) of these attacks had fatal consequences in which all the young and the female (if she was not yet eaten by the young) died. In 52% (n = 42) of all attacks at least some of the spiderlings survived, for example, by moving into the web during the attack. Initial average brood size was 22

(underestimated because not all spiderlings can be seen without destruction of the nest); and in the attacked broods with survivors, a median of nine spiderlings dispersed. Most of these attacks occurred after the female had died, or if the female was still alive she fell victim, too. In four cases, females lost all their young shortly after hatching. None of these four females lived long enough to complete a second reproductive event, and two made a replacement clutch but died before these young hatched. Of 127 nests with young, 31.5% were attacked by spiders, 21.3% by ants, 5.5% by birds, and 5.5% by unknown predators. The main predator in the hatchling period was the spider *Poecilochroa senilis* which was responsible for 49.3% (n = 40) of all attacks.

Comparison of the two periods.—The survivorship functions of the two periods differ in their slopes. Survival probabilities are higher during the hatchling period than during the egg period (Fig. 3). Survivorship for the first 25 days of each period was compared using the method recommended by Hutchings, Booth & Waite (1991). The actual number of animals that died each day is compared to an expected number of dead animals for each day (derived by assuming an even probability of death for animals in both samples). The result gives a χ^2 value of 16.88 (df = 1, P < 0.001); thus, the hypothesis that mortality rates were the same in both phases is rejected. A χ^2 test using the actual number of spiders that died over the two periods gives the same result as the above method. During the egg period 54.3% (151 of 278, including 6 females that never reproduced successfully) of all females had no reproductive success compared to 30.7% (39 of 127) of the females in the hatchling period (χ^2 = 16.9, df = 1, P = 0.0001). During the egg period, females suffered a 14% risk of becoming parasitized by the wasp *P. humboldti*. This wasp never parasitizes females with young, presumably because the spiderlings would feed on the female even if she is paralyzed and would therefore kill the wasp larva, too. This might explain a part of the 23.6% lower mortality rate during the hatchling period. Although a high percentage of nests was attacked during the hatchling period (n = 81 and 63.8%, compared to 61% and n = 169 during egg period), many of the attacks did not result in death of the whole brood. This is because spiderlings are mobile so that often some young could escape an attack, whereas the entire clutch is lost if the egg sac is opened. Additionally, the young are not able to leave the cocoon without the help of the mother so that they have no chance of survival if the mother dies before hatching.

DISCUSSION

Stegodyphus lineatus females are vulnerable to predation and parasitism. Adult females fall victim to birds, ants, parasitoid wasps, and other spiders. Only 27% of the adult females in the population raised young which successfully dispersed. Of these females, 50% had a reduced reproductive success because predators caused the death of some of the brood. Daily survival probabilities stayed the same throughout the season so that females that reproduce fast have a higher chance of completing reproduction than do females that take longer. Usually, a trade-off between body size and time of reproduction will produce a situation where a female spider reproduces early and small or late and large (Vollrath 1987). In *S. lineatus*, however, large females reproduced earlier than smaller ones although they were all mature at the beginning of the study period. Small females had reduced fecundity because clutch size is a function of body mass in *S. lineatus* (Schneider 1992), and they were also exposed to predation for a longer period of time. Females with high growth rates had the combined advantages of increased fecundity and early reproduction. Spiderlings that hatched early had a high survival probability before dispersal and also more time to feed and grow before prey availability declined in the dry summer.

The significance of body size for the reproductive value of offspring might be one explanation for the high maternal investment in individual offspring. Bigger spiderlings had higher survival probabilities during periods of low prey availability (Schneider 1992), and they may have had an initial foraging advantage with a cumulative effect through time (Schneider 1995). Larger spiders build relatively larger webs, and larger webs catch more prey (Ward & Lubin 1993). Larger spiderlings are more likely to mature early as large adults and therefore have a higher reproductive value. Because of the advantages of early growth for future survival and fecundity, I suggest

that there is selection for small clutches and extended maternal care. Correlations between body size and several traits relevant to fitness, such as mating success for males or time to maturation, are also known for other spider species (Vollrath 1987).

The period of egg development was riskier than the hatchling period, which is in accordance with Shine's (1978) explanation of the evolution of small eggs. If a female survived until her young had left the cocoon, her chances of successfully completing reproduction increased. The wasp *P. humboldti* was responsible for 14% of the mortality in the egg period. In an earlier study in the same area, the rate of parasitism was as high as 25.6% (Ward & Henschel 1992). In general, wasp predation varied between 14–29% depending on the density of the spiders (Schneider 1992; Ward & Henschel 1992; Henschel et al. 1996). Spiders suffered less predation during the hatchling period, both because wasps did not attack during this stage and because attacks by spiders or ants were less fatal then. A possible way of reducing the risk of wasp predation would be to shorten the period of time during which the spiders suffer the highest risk of parasitism: the shorter the interval between molting and egg-laying and the faster a female's eggs hatch, the greater is her probability of survival. Given that all physiological parameters stay constant, a decrease in the amount of yolk decreases egg size and the duration of the egg stage for poikilotherms (Sinervo 1990). A few studies have actually shown that big eggs that are provisioned with a large amount of yolk take longer to develop when compared to smaller eggs with less yolk (reptiles: Sargent et al. 1987; crustaceans: R. Diesel, pers. comm.). A more critical test of this relationship showed that egg development was shortened when the amount of yolk was reduced experimentally, and the young hatched at an earlier stage in their development or at a smaller size (Brestowsky 1968; Sinervo 1990; Sinervo & Licht 1991; Bernardo 1991 and references therein). Further studies are needed to determine whether the relatively low yolk content of *S. lineatus* eggs speeds hatching.

S. lineatus spiderlings are unable to survive without the care of the mother. Their bodies are very soft, almost translucent and without hair. As a result, their abdomen can expand enormously and growth rates are fast during the period when the females provide food via regurgitation (Schneider 1992). Although the eggs are relatively small in *S. lineatus*, egg development still takes longer than the hatchling period. Eggs seem to develop in a time similar to spiders from other families (such as Theridiidae, Araneidae and Agelenidae) where, depending on the temperature, egg development takes between 10 days (30 °C) and 50 days (10 °C) (Foster & Kingsford 1983; Pulz 1987). The question arises whether the species has reached the lower limit in egg size or whether egg size is a phylogenetic constraint. Data on other species of Eresidae are needed to distinguish between these possibilities and to study the evolution of egg size and maternal care in this group.

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RESEARCH NOTE

A THIRD SPECIES OF THE GENUS *MEXICHTHONIUS* (PSEUDOSCORPIONIDA, CHTHONIIDAE), FROM A CAVE IN TEXAS

The genus *Mexichthonius* was established with the description of *Mexichthonius unicus* Muchmore 1975; the holotype (a female) and only known specimen of this species was taken from under a rock at Ich-Ek, Campeche, Mexico. A second representative of the genus, also a female, was found in rotted wood near Palenque, Chiapas, Mexico, and was described as *Mexichthonius pacal* Muchmore 1978. No other material pertaining to the genus was known until recently, when a single specimen, this time a male, was collected in a cave in Travis County, Texas, USA.

Genus *Mexichthonius*

Mexichthonius Muchmore 1975: 1–2. Type species *Mexichthonius unicus* Muchmore 1975, by original designation.

Diagnosis (emended).—With the description of the new species, below, it is necessary to change the generic diagnosis slightly. *M. exoticus* agrees well with the other two species in all characters but two: 1) in *M. exoticus*, the lateral seta on the apex of the palpal coxa is essentially straight, while the corresponding seta in the other two species is sharply curved medially, and 2) in *M. exoticus*, each finger of the palpal chela is provided with well developed teeth along the entire margin, while in the other two species each finger possesses only a few distinct teeth distally, followed proximally by a series of low irregularities of the margin. In addition, in all three species the small, medial members of the coxal spines are difficult to make out, but they are probably more scale-like than hair-like.

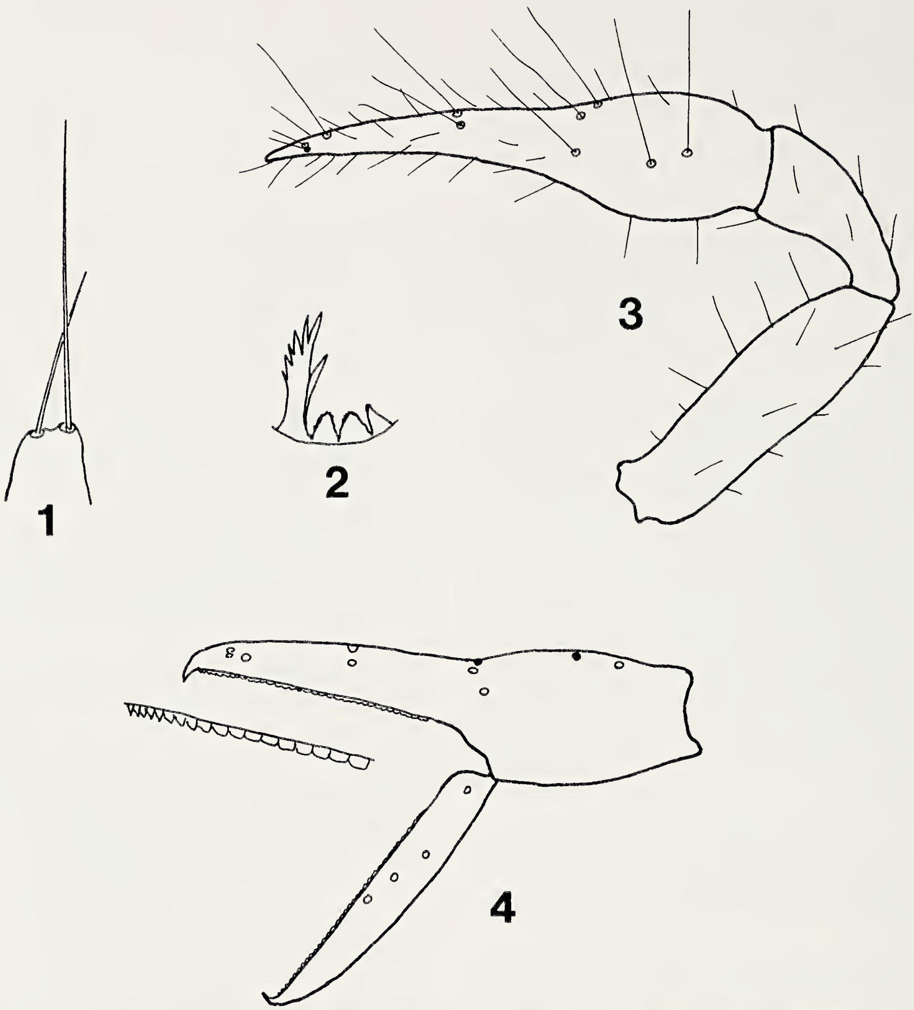
Mexichthonius exoticus new species
(Figs. 1–4)

Type.—Male holotype (WM7936.01001) from Five Pocket Cave, Travis County, Texas, 9 November 1993 (Keeley and Horvath); mounted on slide, in Florida State Collection of Arthropods, Gainesville, Florida.

Diagnosis.—Very similar to *M. unicus* and *M. pacal*, but with the lateral seta on apex of palpal coxa straight instead of strongly curved, and with well developed teeth all along margins of both chelal fingers.

Description.—*Male:* (female unknown). With the characters of the genus and the following particular features. Palps tan, other parts straw-colored. Carapace a little longer than broad; epistome broad, serrate; no eyes; chaetotaxy 6–4–4–2–2. Coxal area mostly typical of the genus; apex of palpal coxa (Fig. 1) with two setae, the lateral one shorter than the medial one and nearly straight; apex of coxa I with three microsetae; coxa II with one large, complex coxal spine laterally and 3–4 small, flattened spines medially (Fig. 2). Abdomen typical; tergal chaetotaxy 4:4:6:6:6:6:6:6:6:4:T2T:0; chaetotaxy of sternites 2–4 is 8:(2)5–4[?]/8 (2):(2) 6 (2):-. Chelicera 0.7 as long as carapace; hand with five setae; flagellum of about eight pinnate setae; galea a small knob. Palp (Fig.3) rather robust; L/B of trochanter 1.9, femur 3.5, patella 1.9, and chela 3.8; L/D of hand 1.55; movable finger L/hand L 1.55. Trichobothria typical of the genus (Fig. 4), with *isb* and *ib* in tandem on dorsum of hand and *t*, *st* and *sb* closely grouped at middle of movable finger. Fixed finger with about 40 teeth, mostly rectangular but smaller and taller distally (Fig. 4); movable finger with about 35 similar teeth; fixed finger with one internal accessory denticle at level of third tooth. Legs typical, stout.

Measurements (mm): Body L 1.03. Carapace L 0.31. Chelicera L 0.215. Palp: trochanter 0.125/0.065; femur 0.28/0.08; patella 0.17/0.09;



Figures 1–4.—*Mexichthonius exoticus* new species, male holotype. 1, Apex of right palpal coxa, ventral view; 2, Coxal spines on right coxa II; 3, Right palp (trochanter missing), dorsal view; 4, Left chela, lateral view, showing positions of trichobothria (darkened areoles are underneath), with detail of teeth on distal half of fixed finger.

chela 0.42/0.11; hand 0.17/0.11; movable finger L 0.265. Leg IV: femur + patella L 0.27.

Etymology.—The name *'exoticus'* refers to the occurrence of this species far from its congeners.

Remarks.—The new species is very similar to *Mexichthonius unicus* and *M. pacal*, especially in the unique placement of trichobothria *ib* and *isb* on the dorsum of the chelal hand and in the unusual structures of the coxal spines. It differs only slightly from them – in the shape of the lateral seta on the apex of the palpal coxa which is straight rather than sharply curved, and in the possession of well-developed, rather than obsolescent, teeth along the entire margins of both chelal fingers. It is, without doubt, a representative of *Mexichthonius*.

As *M. unicus* and *M. pacal* are both from southern Mexico (Campeche and Chiapas, respectively), it is quite surprising to find *M. exoticus* in Texas, some 2500 km to the north. Presently extant populations of *Mexichthonius* may actually be separated by this great distance, but it seems much more likely that other populations exist in between, undiscovered because of their minute size and the general lack of collecting of soil faunas in that area.

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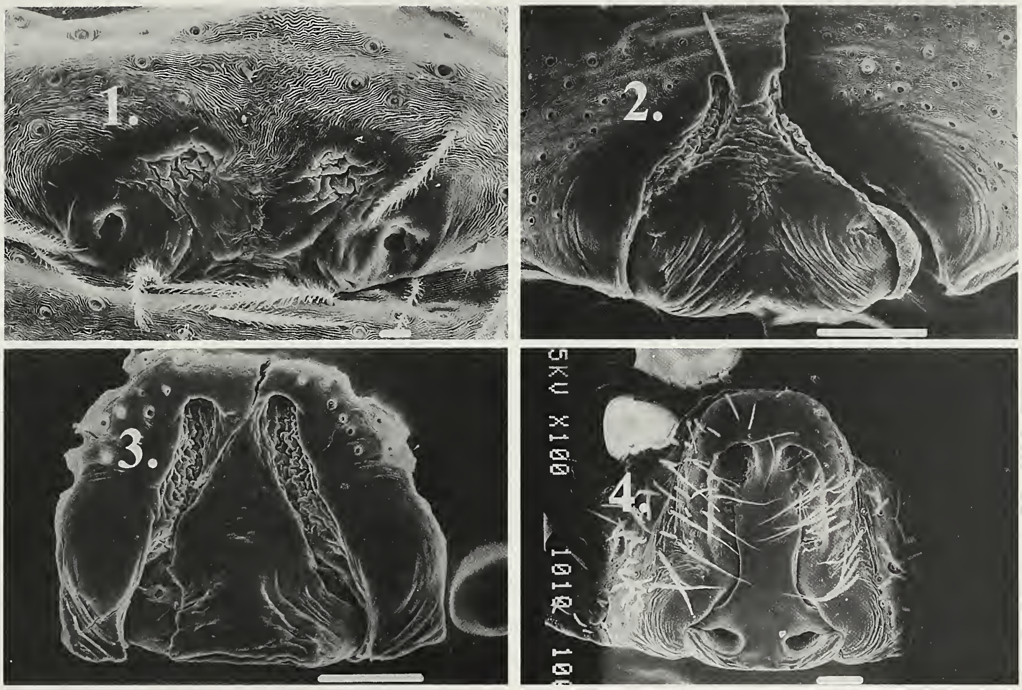
RESEARCH NOTE

A METHOD FOR ASSESSING GENDER IN IMMATURE WOLF SPIDERS (ARANEAE, LYCOSIDAE)

> "Araneists may well be advised to abandon their traditional habit of neglecting or even throwing away the immature specimens that they find, for these have much to teach us, and even the cast-off exoskeletons left after moulting may be profitably examined."
>
> Theodore Savory (1977)

Male and female spiders are typically distinguished by external characters (pedipalps and epigyna) of mature individuals. Texts concerning the biology of spiders (Savory 1928; Gertsch 1949; Foelix 1982; but see Comstock 1948: 130) do not mention ontogenetic variation in these structures although such variation has been known to systematists for many years (Strand 1906; Bhatnager & Rempel 1962; Sadana 1972; Levi 1982; Lachmuth et al. 1985; Sierwald 1989). This phenomenon has been largely unknown to the many ecologists working with spiders or, if known, the earliest stages of the ontogeny of epigynal structures have been unknown in spite of their potential utility. For example, of 69 papers published in volumes 19–20 of the Journal of Arachnology, 16 ecological papers dealt with spider species which had no obvious sexual dimorphism prior to the penultimate instar. These studies might have benefited from knowledge of the gender of immature individuals for a variety of reasons. Field studies concerned with habitat distribution and dispersal could benefit from knowing if male and female juveniles are distributed evenly in the habitat. In experimental studies, the two sexes should be balanced among treatments in order to account for differences due to sex. This would be particularly important in studies of growth rate where allocation rules may differ between sexes. In studies of sex ratio evolution, the predicted sex ratio of 1:1 may change through the development of a cohort resulting from differential selection acting on juvenile males and females. Therefore, knowledge of the gender of individuals can be very important to increasing our understanding of the ecology of spider species if it should prove not too difficult to gain. Herein, we describe a method to distinguish gender based on the ontogenetic development of the epigynum of the wolf spider, *Schizocosa ocreata* (Hentz 1844).

From 30 June–3 July 1994 we collected 22 female *S. ocreata* from the Stephen F. Austin Experimental Forest (7.5 km SSW of Nacogdoches), Nacogdoches County, Texas. We returned these females to the lab where they laid egg sacs and hatched young. We reared these young to maturity on an *ad libitum* diet of lab-reared crickets (*Acheta domestica*) in a temperature controlled room (26.1–27.7 °C) on a 14:10 light:dark cycle. We recorded the date of each molt for all individuals which allowed us to know how many instars prior to maturity an individual had been measured. In March of 1995, when the range of variation in development extended from the 7–12th instar beyond the deutovum stage, we began measuring the length and width of the epigynum of all individuals. We accomplished this by placing individuals in three dram shell vials and squeezing them to the bottom of the vial with a plug of cotton, after which we examined under a dissection microscope (63×) the abdomen between the book lungs for signs of epigynal development. All measurements were taken by the junior author. If a pre-epigynum was evident, an optical micrometer was used to measure its length and width from the extreme edges of the raised, sclerified portion of the epigynum (see Figs. 1–4). In addition, we ex-

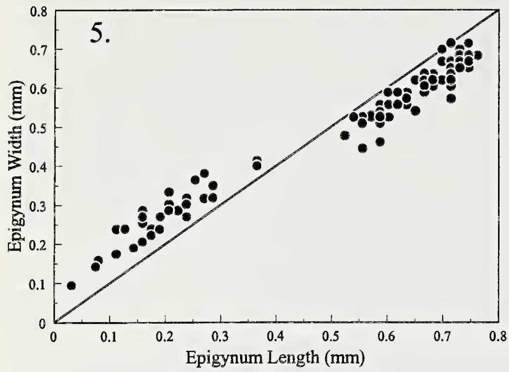


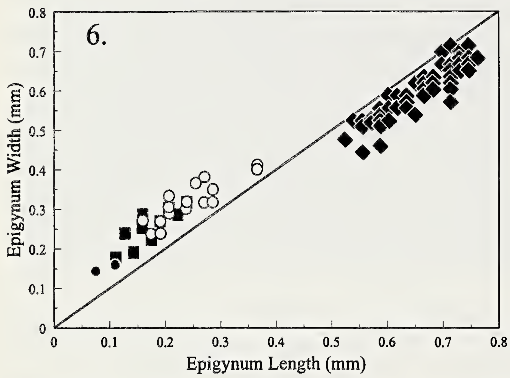
Figures 1–4.—Scanning electron micrographs illustrating the ontogeny of epigynal structures of *Schizocosa ocreata* (Hentz). 1, Third instar, scale bar = 10μm; 2, Three instars prior to maturity, scale bar = 100μm; 3, One instar prior to maturity, scale bar = 100μm; 4, Adult, scale bar = 100μm.

amined alcohol-preserved individuals from the first instar through maturity to determine the earliest age at which the pre-epigynum appears. We constructed plots of epigynum width versus epigynum length for all individuals as well as plots of epigynum width versus epigynum length for individuals for which we had two or more measures during ontogeny. We scored individuals without a pre-epigynum as "absent" (n = 15) and predicted them to be males. We tested this prediction as the individuals grew to maturity. All immatures that were scored as "absent" subsequently matured into adult males at instars similar to their female siblings.

Although the measures we employed were crude (epigynum length and width), we can distinguish immatures and matures based on their epigynum morphology. Mature individuals possess an epigynal structure that is longer (mean = 0.66, SD = 0.06) than wide (mean = 0.60; SD = 0.06) (Figs. 4, 5) while immature individuals possess an epigynum that is shorter (mean = 0.20, SD = 0.07) than wide (mean = 0.27, SD = 0.07) (Figs. 1–3, 5). The immature epigynal structure appears in individuals as early as the third instar as an isosceles triangle bisected from anterior to posterior with what appears to be a precursor to the median septum (Fig. 1). The pre-epigynum maintains this structure until the third or fourth instar prior to maturity at which time the sclerification and lengthening begins (Figs. 2–3). Figure 6 shows that epigynal morphology cannot be used to predict the number of instars remaining to maturity, nor is the instar at which maturity is reached related to the overall size of the epigynum (data not shown).

We have demonstrated a method for determining gender that can be used to distinguish between the sexes in juveniles of the wolf spider *Schizocosa ocreata.* More importantly, this method is simple (requiring only a dissecting scope with 20× magnification for identification; higher if measurements are to be made) and could be utilized in the field with live individuals unlike the chromosomal methods of Avilès & Maddison (1991) which require the death of the specimen. In addition, pre-epigyna can be viewed in exuvia of spiders (field caught and lab-reared) by the methods of Sierwald (1989). The appearance of external pre-epigyna in immature spiders is





Figures 5–6.—Plots of epigynal width versus epigynal length. 5, All individuals which were measured; 6, Epigynal measurements at different numbers of instars prior to maturity. ● = three instars prior to maturity; ○ = antepenultimate instar; ■ = penultimate instar; ◆ = adults. For both figures, the solid line represents a 1:1 relationship between the two measures. Adults fall on or below the line while immatures fall above the line.

common in the Lycosoidea (Sierwald pers. comm.) including the Pisauridae (Sierwald 1989), Psechridae (Levi 1982) and the Agelenidae (Strand 1906). The pre-epigynum is visible internally in the exuvia of the Theridiidae (Bhatnager & Rempel 1962).

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RESEARCH NOTE

ESTIMATING LIVE SPIDER WEIGHT USING PRESERVED SPECIMENS

The feasibility of estimating live weight from preserved material is examined. One option for estimating live weight is presented by Greenstone et al. (1985a, b), where an estimated volume was determined by a series of measurements of several body dimensions which were then compared with the actual weight of specimens. This procedure involved extended manipulation of specimens and equipment. Rogers et al. (1977), using recently preserved specimens ("a few weeks later") calculated length-weight relationships for a variety of insects and spiders. They noted that "Clearly, power functions adequately describe length-weight relationships for adult invertebrates and for immature taxa exhibiting simple metamorphosis (nymphs)".

This study examines the degree to which preserved material using a power function provides useful data. The bulk of preserved material used was collected in 1989 and 1990 on Cape Cod, Massachusetts in connection with another study (Edwards 1993). Collection details are provided therein. A few specimens were collected earlier. All were preserved in 75% denatured ethanol, and all had their alcohol replaced at least once, typically within 48 hours of collection. The total length was measured from the clypeus to the distal tips of spinnerets, using an ocular micrometer for specimens <12 mm and vernier calipers for those >12 mm. The total length was measured to the nearest 0.1 mm, and the specimens damp dried on absorbent paper before weighing. Distorted

Table 1.—Fresh and preserved spiders examined. Number of individuals = n, lengths included in sample = range (mm).

	Preserved specimens			Fresh specimens		
Taxa	n	Genera	Range (mm)	n	Genera	Range (mm)
Agelenidae	39	3	3.0–13.5	25	5	4.5–13.5
Anyphaenidae	33	4	2.4–8.4	28	4	2.7–8.5
Araneidae	28	5	2.1–21.2	48	8	2.4–21.2
Clubionidae	27	7	2.5–9.0	40	5	2.2–8.8
Gnaphosidae	48	7	3.0–13.1	49	5	2.8–10.1
Linyphiidae	23	6	1.9–6.5	24	8	1.5–5.5
Lycosidae	19	7	4.0–21.5	50	9	2.0–23.5
Philodromidae	26	3	2.5–8.6	24	3	2.0–7.0
Pisauridae	9	2	2.0–12.5	7	2	4.0–11.1
Salticidae	24	3	4.0–13.0	46	7	4.0–10.1
Tetragnathidae	26	1	3.5–9.0	19	1	2.5–7.8
Theridiidae	33	6	1.5–7.5	42	7	2.1–7.6
Thomisidae	57	5	1.8–8.0	50	6	1.9–8.3
Total	405	59		454	70	
Random sample	300	59	1.8–21.5	300	70	1.5–23.5

Table 2.—Statistical parameters for spider weight-length equations, *ln weight* = *a* + *b*(*ln length*), for fresh and preserved material. Number of individuals = *n*, standard error = SE, coefficient of determination = r^2. Random sample taken from total data pool.

	n	a	SE a	b	SE b	r^2
Preserved specimens						
Agelenidae	39	−1.939	0.248	2.757	0.084	0.966
Anyphaenidae	33	−2.077	0.299	2.816	0.143	0.926
Araneidae	28	−1.512	0.329	2.760	0.102	0.966
Clubionidae	27	−1.599	0.287	2.542	0.166	0.903
Gnaphosidae	54	−2.616	0.301	3.008	0.152	0.905
Linyphiidae	23	−1.504	0.181	2.569	0.270	0.812
Lycosidae	19	−1.480	0.187	2.647	0.090	0.981
Philodromidae	26	−1.480	0.271	2.680	0.189	0.893
Pisauridae	9	−1.243	0.234	2.633	0.122	0.985
Salticidae	24	−1.611	0.290	2.782	0.180	0.916
Tetragnathidae	26	−1.243	0.281	2.119	0.219	0.795
Theridiidae	33	−1.229	0.232	2.697	0.105	0.955
Thomisidae	57	−1.655	0.220	2.986	0.086	0.957
Average	29.5	−1.630	0.259	2.692	0.147	0.920
Random sample	300	−1.533	0.420	2.651	0.051	0.901
Fresh specimens						
Agelenidae	25	−2.031	0.235	2.660	0.097	0.957
Anyphaenidae	28	−2.247	0.244	2.814	0.139	0.940
Araneidae	44	−1.923	0.434	2.923	0.111	0.938
Clubionidae	40	−2.156	0.188	2.653	0.102	0.947
Gnaphosidae	49	−2.830	0.200	3.055	0.098	0.954
Linyphiidae	24	−1.829	0.382	2.754	0.216	0.881
Lycosidae	50	−2.043	0.280	2.842	0.083	0.961
Philodromidae	24	−1.985	0.177	2.940	0.114	0.968
Pisauridae	7	−2.040	0.133	2.847	0.141	0.988
Salticidae	46	−2.184	0.238	2.901	0.150	0.895
Tetragnathidae	19	−2.615	0.186	2.574	0.144	0.950
Theridiidae	42	−1.577	0.268	2.907	0.105	0.951
Thomisidae	50	−1.644	0.294	2.973	0.132	0.914
Average	33.1	−2.098	0.237	2.845	0.126	0.946
Random sample	300	−1.844	0.506	2.711	0.053	0.898

specimens were not used. In those cases where the pedicel had elongated, the measurement was corrected for the separation of the thorax from the abdomen. All the measurements of preserved material were carried out in 1993 and 1994. Specimens of all the species used in this study have been deposited in the United States National Museum.

The fresh material for this study was collected in the months of June—September in 1993 and 1994 from the same area and habitats as the preserved material. The collections were made in the afternoon, the spiders immobilized in an ethyl acetate collecting jar, identified and measured to the nearest 0.1 mm in the evening, refrigerated overnight at 3 °C, and weighed the following morning on a Mettler A200 balance, accurate to 1 mg.

The families, genera, number of individuals weighed, and the range of total lengths are provided in Table 1. To the extent possible, for both preserved and fresh samples, the range of lengths used for each family was matched and included immatures and adults. A total of 1021 fresh and preserved specimens representing 79 genera and 13 families was weighed (Table 1). In addition, a random sample of 300 fresh weights and 300 preserved weights was selected from the data described above for separate analysis.

The weight-length equations obtained are included in Tables 1 and 2 in the category 'Random sample'.

The equation, *ln weight = ln a + b (ln length)*, was used to estimate weight at length. The results are provided in Table 2. The coefficient of determination (r^2) for the equations ranged from 0.795 (Tetragnathidae preserved) to 0.988 (Pisauridae fresh), with five less than $r^2 = 0.900$. The average values for constant a (intercept) and exponent b (slope) were less for preserved specimens than fresh specimens. The equations calculated using the randomly selected, large sample vary similarly. Variations in the weight of spiders at any particular size or instar or varying seasonal conditions have been documented by many authors, e.g., Jocque (1981) and Edgar (1971). It will be noted that the r^2 values for the samples in Table 2 suggest that the data were reasonably well fitted by the power function.

The relationship between exponent b for preserved spiders with b for fresh material was significant, $r^2 = 0.619$, ($F_{11,1} = 17.89$; $P < 0.01$) (Fig. 1A). Constant a for both preserved and fresh were barely significantly related, $r^2 = 0.287$, ($F_{11,1} = 4.44$; $P = 0.061$) (Fig. 1B). The lack of any relationship between coefficient b and constant a, $r^2 = 0.001$, for fresh material comes as no particular surprise. Different families generally have characteristic body shapes. A mix of genera with differing body shapes within a family, for example the Therididae with the stout-bodied genus *Steatoda* Sundevall 1833, and the relatively longer-legged, globular-bodied genera like *Achaearanea* Strand 1929, and *Theridion* Walckenaer 1805, make it desirable to consider basing the weight-length equations on genera. Although such genera may share a similar b exponent, they can differ considerably in weight at length (Edwards unpubl. data).

Rogers et al. (1977) calculated a length-weight equation for Araneida, based on 25 specimens not identified to genus or family, where

$$ln\ weight = -3.106 + 2.929\ (ln\ length).$$

In this study the equation based on the random sample values for preserved specimens is

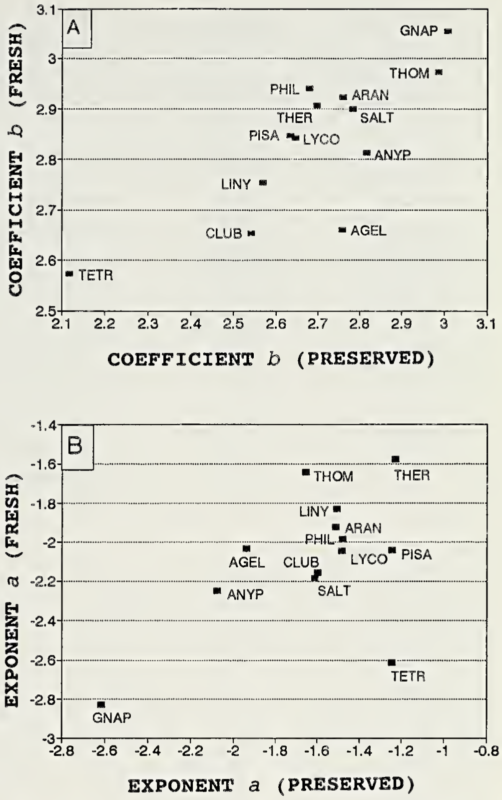

Figure 1.—Comparisons of the statistical parameters for the equation *ln weight = ln a + b (ln length)* for fresh and preserved spiders. The points shown are identified by the first four letters of the taxa listed in Table 1. A. Coefficient b (slope) for preserved material compared with coefficient b for fresh. B. Constant a (intercept) for preserved material compared with constant a for fresh material.

$$ln\ weight = -1.533 + 2.651\ (ln\ length)$$

and for fresh material is

$$ln\ weight = -1.844 + 2.711\ (ln\ length)$$

One general conclusion that may be drawn is that both fresh and preserved spiders tend to increase their length somewhat faster than they accrue weight (exponent $b < 3$) and that spiders preserved (in denatured alcohol at least) weigh more than live spiders.

To illustrate the potential usefulness of comparing different habitats in terms of preserved weight, data on the spiders taken from the trunks of pitch pine and scarlet oak are compared. Species of ten families contribute ±99% in numbers of spiders on these tree

Table 3.—Percent numbers and weight/quadrat in milligrams (mg) of spiders by family for Scarlet Oak and Pitch Pine trunk collections; 41 and 35 0.25 m^2 quadrats respectively. Percent number of individuals = *n*, weight preserved = p, weight fresh = f and ratio of fresh/preserved = f/p.

	%*n*	p, mg	f, mg	%p	%f	f/p
Pitch Pine trunk						
Araneidae	15.3	3.8	3.0	6.5	6.3	0.80
Clubionidae	8.1	5.3	3.8	9.1	8.0	0.72
Erigoninae	14.8	1.7	1.4	2.9	2.9	0.81
Gnaphosidae	2.6	2.3	2.0	3.9	4.2	0.88
Linyphiidae	1.7	0.2	0.2	0.4	0.4	0.83
Lycosidae	1.2	9.3	8.1	16.0	17.0	0.87
Philodromidae	12.7	9.9	8.6	17.1	18.1	0.87
Salticidae	5.3	15.0	10.7	25.8	22.6	0.71
Theridiidae	28.2	4.4	3.6	7.7	7.6	0.81
Thomisidae	8.9	6.1	6.1	10.5	12.8	1.00
Total	98.8	58.0	47.5	100.0	100.0	
Average						0.831 ± 0.0817
Scarlet Oak trunk						
Araneidae	11.0	3.7	3.0	5.6	5.5	0.80
Clubionidae	16.7	26.5	18.8	39.9	35.3	0.71
Erigoninae	12.9	1.8	1.5	2.7	2.8	0.83
Gnaphosidae	1.5	2.5	2.2	3.8	4.2	0.89
Linyphiidae	16.0	0.3	0.3	0.4	0.6	1.07
Lycosidae	1.7	20.9	18.8	31.5	35.3	0.90
Philodromidae	0.8	0.3	0.2	0.5	0.5	0.80
Salticidae	3.5	2.8	1.8	4.2	3.4	0.66
Theridiidae	34.2	5.9	5.0	8.9	9.3	0.84
Thomisidae	0.8	1.7	1.7	2.6	3.2	0.98
Total	99.1	66.4	53.2	100.0	100.0	
Average						0.847 ± 0.1211

trunks (see Table 3). The collection details for the habitats used in this comparison are provided in Edwards 1993. Weights were calculated using the appropriate weight-length parameters for fresh and preserved specimens (Table 2).

The regression of fresh weight on preserved weight had an r^2 of 0.977. Using the random sample equation for preserved material, the habitat comparison data was recalculated. The resulting comparison of fresh *versus* preserved weight had an $r^2 = 0.901$, a statistically significant reduction from the value of $r^2 = 0.977$ obtained using the separate family equations. The results are compared graphically in Fig. 2.

The ratio of fresh weight/preserved weight (*f/p*) for the various families sampled, with a few exceptions, increases as spiders increase in size (Table 4). In the case of the random sample, the difference between fresh and preserved weight ($f-p$) is described by the equation

$$ln(f-p) = -0.836 + ln(f)0.873,$$

$r^2 = 0.999$. The *f/p* ratio increases from 0.76 for weight at an average length of 2 mm to 0.84 at 10 mm, with different families varying considerably, one from the other. Clausen (1983) noted that "the ratio of dry over wet weight increases with decreasing size of the specimens", and suggested that "With decreasing size, the exocuticle may make up a relatively greater part of the animal's weight because of the relatively greater surface". The *f/p* data presented here further support Clausen's suggestion.

The procedure reported here serves to provide a first approximation of weight (biomass) for the purpose of comparing the species assemblages of different habitats. However, there are many potential variables to consider,

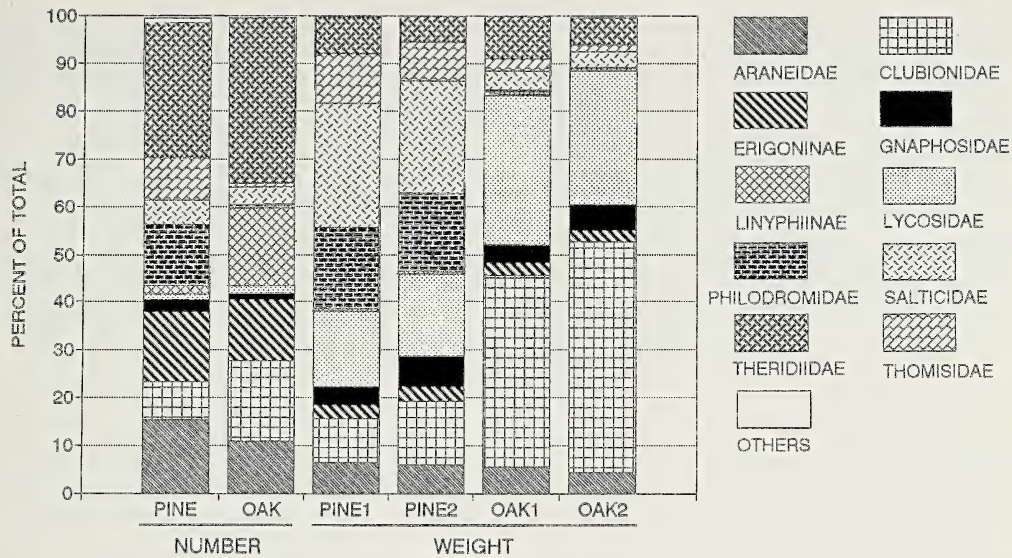

Figure 2.—Graphic comparison of proportional representation of families of spiders by density (number of individuals) and biomass (estimated weight in mg based on preserved specimens) on scarlet oak and pitch pine trunks. The nine families included account for virtually all spiders found in terms of numbers (±99%). The weight calculated using the equations for each family are shown as PINE1 and OAK1, those using the random sample equation labeled as PINE2 and OAK2. The subfamilies Erigoninae and Linyphiinae of the family Linyphiidae, now generally considered of doubtful taxonomic value, are used here to separate the small, rotund genera (e.g., *Ceraticelus* Simon 1884 and *Grammonota* Emerton 1882) from the larger, less rotund genera of the family (e.g., *Drapetisca* Menge 1866 and *Pityohyphantes* Simon 1929).

Table 4.—Ratio of spider fresh weightpreserved weight. Number of genera = genera, number of individuals = *n*. See text for details.

	Length				
	2 mm	6 mm	10 mm	Genera	*n*
Agelenidae	0.83	0.76	0.73	3	39
Anyphaenidae	0.84	0.84	0.84	4	33
Araneidae	0.77	0.90	0.97	5	28
Clubionidae	0.63	0.71	0.74	7	48
Gnaphosidae	0.84	0.88	0.90	7	48
Linyphiidae	0.86	1.02	1.12	6	23
Lycosidae	0.68	0.82	0.90	7	19
Philodromidae	0.77	0.98	1.11	3	26
Pisauridae	0.55	0.67	0.74	2	9
Salticidae	0.63	0.70	0.74	3	24
Tetragnathidae	0.38	0.59	0.74	1	26
Theridiidae	0.76	0.82	0.84	6	33
Thomisidae	1.00	0.99	0.98	5	57
Average	0.73	0.82	0.87	–	–
Random sample	0.76	0.82	0.84	59	300

not the least of which are the varied methods of preservation and the mix of instars and genera included in the sample. The degree of consistency found here between preserved weight and fresh weight is, however, encouraging.

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RESEARCH NOTE

UNA PROBABLE ESTRATEGIA PARA INSEMINAR MAS HEMBRAS EN MACHOS DE *BOTHRIURUS BONARIENSIS* (SCORPIONES, BOTHRIURIDAE)

En los escorpiones, el tiempo que requieren los machos para regenerar los hemiespermatóforos después del apareamiento varía entre las especies (Polis & Sissom 1990). Este puede ser de sólo cuatro días (Benton 1992, 1993) o insumir más de dos semanas (Bücherl 1956; Shulov & Amitai 1958; Peretti 1991). En *Bothriurus bonariensis* (C. L. Koch 1843), especie típica de la región pampeana de Argentina (Peretti 1992, 1995), este proceso demanda entre tres y siete días (Peretti 1993). Recientemente, Matthiesen (1993) ha realizado observaciones sobre la predisposición al cortejo en los machos de *Tityus bahiensis* (Perty 1834), después de extirparles parte de sus hemiespermatóforos, glándulas accesorias e inclusive testículos. Yo sugerí que los machos de *Bothriurus bonariensis* cuya predisposición para cortejar no dependiera del grado de regeneración de los hemiespermatóforos, tendrían alguna ventaja en la inseminación de las hembras sobre los que sí dependen (Peretti 1993). El presente trabajo investiga la conducta sexual que exhiben los machos de esta especie a lo largo del proceso de regeneración de sus hemiespermatóforos.

Se utilizaron un total de 36 machos y 36 hembras capturados entre 1990 y 1993 en la localidad de Mendiolaza, Provincia de Córdoba. Los ejemplares de referencia ("voucher specimens") de este estudio han sido depositados en la Colección de Referencia de la Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina. Durante las observaciones la temperatura ambiente osciló entre 24–36 °C. La iluminación provino de una lámpara incandescente (25 W) ubicada a 50 cm de distancia del terrario. A partir de la culminación de un apareamiento -día 0- y hasta completar el proceso de regeneración (valor previamente registrado en la población: $\bar{x} \pm SE = 5.0 \pm 0.7$ días, $n = 29$) se colocó a cada macho experimental en un terrario de $50 \times 50 \times 15$ cm junto con una hembra receptiva (ésta se reconoce porque antes se probó que aceptaba cortejar), registrándose en cada prueba si el macho realizaba el cortejo y la transferencia espermática.

Todas las pruebas fueron monitoreadas continuamente hasta que la inseminación se realizara o la pareja se separara; todas las conductas se registraron mediante relato grabado en cassettes de audio. Para verificar si la inseminación se efectuó o no, y el tiempo preciso en que ocurrió, se observó bajo lupa al espermatóforo post-inseminación (éste nunca fue comido por el macho o la hembra). Sólo se tuvieron en cuenta los cortejos que nunca se interrumpieron, de otro modo sería considerado erróneamente como un sólo apareamiento si la hembra es nuevamente asida por el mismo macho (en condiciones de campo seguramente ella escaparía).

Para el presente trabajo se disecaron 11 machos con el fin de verificar el estado progresivo de regeneración de sus hemiespermatóforos. Para cada macho experimental se anotó el número total de inseminaciones que realizó durante los 40 días de observaciones. Estos registros se realizaron en diciembre y enero, meses de mayor actividad sexual. En un estudio previo (Peretti 1993) se comprobó que en estos meses no existe variación en la predisposición sexual de los machos; esta variación ocurre a finales de la estación reproductiva -mes de marzo-. Además, nuevas observaciones (Peretti & Castelvetri obs.

Tabla 1.—Valores numéricos de los tres grupos de machos de *Bothriurus bonariensis* que fueron identificados según su receptividad al cortejo durante el proceso de regeneración de los hemiespermatóforos.

			No. de inseminaciones	
Grupo de ♂	% en el total de ♂ (n = 32)	% de ♂ que realizan transfer espermática (por lo menos 1 vez)	Total del grupo de ♂	Individual ($\bar{x} \pm$ SE)
A	43.7	78.6 (11/14)	19	1.3 ± 0.9
B	31.3	80.0 (8/10)	21	2.1 ± 1.3
C	25.0	87.5 (7/8)	28	3.5 ± 1.7

pers.) indican que en *B. bonariensis* los machos adultos sólo viven una temporada reproductiva.

Al analizar las pruebas de receptividad y disecciones complementarias, se identificaron tres grupos de machos: A) machos que comenzaron a cortejar recién una vez completada la regeneración de los hemiespermatóforos (43.75%); B) machos que comenzaron a cortejar aproximadamente desde la mitad del proceso de regeneración (31.25%), y C) machos que comenzaron a cortejar desde el inicio de la regeneración de los hemiespermatóforos (25%). Existe una cierta graduación intermedia entre estos tres grupos, ya que algunos machos comienzan a cortejar entre el inicio y mitad del proceso de regeneración, en tanto otros lo hacen entre la mitad y el final. En los grupos "B" y "C" (Tabla 1) la mayoría de los machos continuaron cortejando hasta completar la regeneración. Existen diferencias significativas entre el número de inseminaciones conseguidas por los tres grupos de machos al final de la temporada de registro, cuando se los compara de a pares (test de Mann-Whitney: $P < 0.001$). A pesar de que el menor porcentaje de los machos se ajustó al patrón del grupo C (Tabla 1), fueron éstos los que obtuvieron el mayor número de inseminaciones, tanto en su totalidad como individualmente (Tabla 1). Esto fue así, a pesar de que ellos tuvieron que continuar con el cortejo durante varios días hasta completar la regeneración de los hemiespermatóforos.

La duración completa del apareamiento fue significativamente mayor en los machos del grupo C ($\bar{x}$ = 5.2 días; $P < 0.002$) que en los restantes (B: $\bar{x}$ = 2.7 días; A: $\bar{x}$ = 53 min). No se observó ninguna diferencia en los patrones de conducta (frecuencia de aparición y duración) o su secuencia entre los tres grupos de machos.

De acuerdo con los resultados obtenidos, queda evidenciado que en *B. bonariensis* los machos no requieren tener ya regenerados sus hemiespermatóforos para intentar cortejar a una hembra. Matthiesen (1968, 1993) ha observado que los machos de *Tityus bahiensis* cortejaban aún después de extirparles los hemiespermatóforos. Dicho autor sugiere que la predisposición sexual podría estar regida principalmente por el estado gonadal y/o por el sistema nervioso central, tal como ocurre en las arañas (Rovner 1967). Sin embargo, considero que todavía no existen datos suficientes para hipotetizar sobre este punto en escorpiones, ya que muy poco se conoce sobre los procesos fisiológicos que controlan las secuencias de comportamiento del cortejo e inseminación.

He podido determinar recientemente en *Zabius fuscus* (Thorell 1877) (Buthidae) que los machos no cortejan si sus hemiespermatóforos están sólo parcialmente regenerados (Peretti 1993). En *B. bonariensis*, existe gran competencia sexual por las hembras (Peretti & Castelvetri obs. no public.); por lo tanto, la estrategia del grupo C posibilitaría a los machos inseminar un mayor número de hembras durante la temporada reproductiva, al asegurar una hembra mucho tiempo antes de que el macho esté en condiciones de formar el espermatóforo.

En la actualidad, en *B. bonariensis* se desconoce si el cortejo en sí mismo o el contacto con una hembra por parte del macho pueden ser factores que aceleren el proceso de regeneración de los hemiespermatóforos. Esta podría ser una explicación alternativa del por qué el grupo C obtuvo un mayor número de inseminaciones en los experimentos. Sin embargo, la duración del apareamiento fue siempre mayor en el grupo C y con un valor casi idéntico al tiempo que demanda la regeneración de los hemiespermatóforos en cualquier macho en ausencia de una hembra; por lo tanto interpreto que no han acelerado a un nivel apreciable la maduración de los hemiespermatóforos.

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BOOK REVIEW

Barrion, A. T. and J. A. Litsinger. 1995. *Riceland Spiders of South and Southeast Asia.* CAB International, Wallingford, England, xix + 700 pp. US$225.00.

This massive volume, containing over 700 large, double-column pages, represents the culmination of almost 20 years' work by the authors, their illustrator Danilo Amalin, and other members of their team at the International Rice Research Institute in Manila. It is primarily a contribution to the original taxonomic literature, containing descriptions (and well over a thousand illustrations) of 342 species; fully three-quarters of the species (and no fewer than eight genera) are described as new. The wide geographic coverage indicated in the title refers to the inclusion of a handful of taxa and records from such areas as Bangladesh, India, China, Thailand, Cambodia, Myanmar, Vietnam, and Indonesia, but 99% of the book is devoted just to those parts of the Philippine spider fauna that happen to have been collected in ricelands, rather than native habitats. It is certainly the first major work on this important part of the world.

The non-systematic sections at the front of the volume are relatively brief: an introduction that provides a short history of Philippine arachnology, a survey of external anatomy that, together with the glossary, provides enough details to allow beginners to use the keys to families and species, and a page on life histories. There is a listing of the 48 Philippine sites, on eight islands, that were sampled; among other techniques, pitfall, malaise, and suction traps were used in the fields. A classification is provided for just 34 families, including eight not actually discussed in the volume (Dipluridae, Tetrablemmidae, Ochyroceratidae, Palpimanidae, Ctenidae, Amaurobiidae, Anyphaenidae, and Prodidomidae), but those 34 families hardly exhaust even the known Philippine fauna (missing are at least the Filistatidae, Segestriidae, Mysmenidae, and Psechridae).

At the end of the volume, there are brief discussions of a few other arachnids (mites, opilionids, and pseudoscorpions) and of spider diversity in Philippine ricelands. About 30 pages are devoted to tiny distribution maps, which fall largely into two classes. A few species, such as several of the tetragnathids, are so widely distributed, and so commonly collected in ricelands, that their maps show dots virtually everywhere. But most of the species treated in the book are represented by very few specimens; I doubt if the mean number of specimens per species actually reaches as high as two, so many maps show just a single dot, and one large map showing the 48 collecting sites would have been more useful. The glossary is followed by a bibliography, an index to species, and 16 color plates of photographs of our favorite creatures. The bibliography is scanty, and overlooks some of the most relevant literature; the authors have even omitted the 1993 "Illustrated Monograph of the Rice Field Spiders of Bangladesh" by C. Okuma, N. Q. Kamal, Y. Hirashima, M. Z. Alam, and K. Ogata (Institute of Postgraduate Studies in Agriculture [Salna, Gazipur, Bangladesh]-Japan International Cooperation Agency Project, Publication 1).

But it is the systematic section that counts here, and one can readily sympathize with the authors' predicament. The magnitude of the task implied by their presumed directive from the authorities at the International Rice Research Institute—to cover all spider species collected in Philippine ricelands—is daunting, perhaps even mind-boggling. I doubt that any arachnologist today would undertake to treat the entire spider fauna of any part of a tropical region in the absence of such an administrative directive. The results must, of necessity, be less than ideal, for no single arachnologist, nor even a pair of workers, can be thoroughly conversant with the systematics of all spider groups, from tarantulas through jumping spiders.

Nevertheless, tackling a task like this requires that the authors at least be aware of the relevant published literature on each of the

families they cover. In several instances, that is clearly not the case with this volume. Perhaps the weakest areas in the book deal with the hunting spiders. The section on gnaphosids, for example, includes several unfortunate lapses. The authors treat the species *Zelotes cavaleriei* Schenkel 1963, originally described on the basis of a female from China; they redescribe the female and describe a male "for the first time." But that Schenkel name was shown, 12 years ago, to be just one of many synonyms of the widespread, synanthropic species *Trachyzelotes jaxartensis* (Kroneberg 1875). Barrion and Litsinger present (without comment) two completely different figures of the epigynum of *Zelotes cavaleriei*, and those two figures represent specimens of two different genera! The epigynum on the right in their fig. 105b is indeed that of *T. jaxartensis*, but the one on the left belongs not to any member of *Trachyzelotes* Lohmander 1944 or *Zelotes* Gistel 1848, but rather to a member of *Setaphis* Simon 1893 (the male they describe is also a *Setaphis*, belonging to a species that is widespread in Africa as well as Asia). Similar lapses in familiarity with the recent literature are their use of such outdated names as *Clubionoides* Edwards 1948 (a junior synonym of *Elaver* O. P.-Cambridge 1898), *Langbiana* Hogg 1922 (a junior synonym of *Mallinella* Strand 1906), and *Hersilia clathrata* Thorell 1895 (a junior synonym of *H. savignyi* Lucas 1836).

Even when they are aware of the literature, the authors sometimes make pointless errors. For example, they assign one of their new gnaphosid species to *Geodrassus* Chamberlin 1922, a North American genus that they acknowledge was synonymized with *Drassodes* Westring 1851 over 20 years ago. They present no evidence whatever that their Philippine spider is related in any way to the type species of *Geodrassus*, and indeed, it is clear that their species has no such relationships; the illustrations of the eye pattern and male palp show a member of the Echeminae, not a member of the Drassodinae at all!

Similar errors occur throughout what the authors anachronistically consider the "Clubionidae"; they assign species to such well-known northern hemisphere genera as *Agroeca* Westring 1862, *Phrurolithus* C. L. Koch 1839, and *Scotinella* Banks 1911, but none of those new taxa are correctly placed. The species described as a member of the liocranid genus *Phrurolithus*, for example, is clearly a member of the corinnid genus *Oedignatha* Thorell 1881 instead, and the name will probably prove to be just a synonym of the widespread type species *Oedignatha scrobiculata* Thorell 1881, already known from India, Sri Lanka, Malaysia, the Seychelles, and Indonesia.

Perhaps even more distressing is the general lack of adequate diagnoses, both for the new species and the new genera. In most cases, new taxa are presented without any reference to previously described ones. For example, early in the volume, a male salticid is described as the new species *Phaeacius mainitensis*. As is typical for the volume, there is a lengthy verbal description, excellent illustrations of somatic characters, and at least adequate figures of the genitalia (although in general the male palpal figures are not up to the high standard of the other illustrations). But there is no diagnostic information to indicate how *P. mainitensis* can be differentiated from any of the other three species already known from the Philippines (*P. alabangensis* Wijesinghe 1991, *P. canalis* Wanless 1981, and *P. leytensis* Wijesinghe 1991), much less from other members of the genus that occur elsewhere. Indeed, from the volume, one cannot determine whether the authors are even aware of all three of those other Philippine species!

Under the changes that are proposed for the next edition of the *International Code of Zoological Nomenclature*, descriptions such as these, which lack informative comparisons to other taxa, will no longer meet even the minimal requirements for legal acceptance as valid taxa. After perusing this volume, I conclude that those changes cannot be enacted too soon. Consider, for example, the new genus *Alaeho*, based on a new species, *A. linoi*, described here from a single male from Luzon. The description of the genus and species fills a large page, but not a word is devoted to determining which "clubionid" subfamily contains the genus, what other genera the animal might be related to, or how one might distinguish *Alaeho* from any other genus. The only thing clear from the authors' treatment is that the animal is probably misplaced in the Clubionidae. A special stay in Purgatory will be required to atone for those of the new species that are described without a single genitalic illustra-

tion (such as *Misumenoides pabilogus* and *Theridion kambalum*).

The lack of diagnostic information sometimes extends even to the authors' own taxa. For example, the authors describe as new a female from Mindanao (*Cheiracanthium tingilium*), but provide no indication of why this specimen is not the female of *Cheiracanthium daquilium*, described 12 pages earlier on the basis of a single male taken in the same province of the same island. No fewer than 12 new species of *Clubiona* Latreille 1804 are described from the same village on Luzon! Are we really to believe that the two single females that are designated as holotypes of new species are not conspecific with any of the nine different males that are also described as new species (for which no females are known)? Surely the relevant null hypothesis here is that all the specimens are conspecific, and additional evidence is required to support each and every increase in the number of species hypothesized.

A similar lack of information concerns synonymies. *Clubiona atwali* Singh 1970, for example, is listed as a junior synonym of *C. drassodes* O. P.-Cambridge 1874, without any indication that this is a new synonymy (it is, as far as I know), without any indication of whether the authors have seen the types of either name (unlikely, I suspect), and without any explanation of the grounds for the new synonymy (whatever they might have been). In another case, an unmarked synonymy even inadvertently sinks a generic name, when *Lycosa arorai* Dyal 1935 (the type species of *Chorilycosa* Roewer 1960) is placed as a junior synonym of *Pardosa sumatrana* (Thorell 1890).

At higher levels, the authors are conservative in, for example, retaining Metidae as a family distinct from Tetragnathidae. As Mark Harvey has discovered, however, Metidae is not available as a family-group name in spiders, for it is preoccupied within the copepods (where it is based on the genus *Metis* Philippi 1843). The proposed changes in the International Code will allow arachnologists to overcome this problem automatically, by simply using the full name, rather than the stem, of the type genus and spelling the spider group as Metaidae or Metainae.

Although the volume will probably produce a fairly large number of new synonyms, it is unlikely to contain any further homonyms, for the authors have often combined Tagalog words to produce names that are, at the very least, unique. I used to think that *Prodidomus papavanasanemensis* Cooke 1972 took the prize for worst-formed spider name, but Cooke's name is downright euphonious compared to the likes of *Clubiona paranghinlalakirta* (not to be confused, of course, with the new *Clubiona parangunikarta*). Some of the etymologies are humorous; *Clubiona krisisensis* refers not to a place name but to a gasoline shortage, whereas *Enoplognatha yelpantrapensis* refers to just what it sounds like. Some of the jokes seem private (*Clubiona topakea* is "Named after systematist with unsympathetic attitudes").

Those with such unsympathetic attitudes might well wonder what review process, if any, this manuscript passed through before it went to press, and whether any competent systematist (sympathetic or otherwise) would have judged it ready for publication in this form. But the task undertaken by the authors was impossible by definition, and their contribution must be evaluated primarily by comparison with other works produced, for similar reasons, in similar parts of the world. Compared, for example, to several such works produced in India, this volume represents a substantial advance in our knowledge of south and southeast Asian cropland spiders. The enormous cost of the volume will probably limit its distribution to a small handful of libraries, and it is likely to be least available to those workers who could most make use of it.

Norman I. Platnick: American Museum of Natural History, New York, New York 10024 USA.

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(revised October 1996)

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Figures 1–4.—*A-us x-us,* male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us,* holotype male; 33, 34, *A-us y-us,* male. Scale = 1.0 mm.

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Cover illustration: Tengella radiata (Tengellidae) on web along forest trail at La Selva, Costa Rica. Taken with Olympus OM-1 with 50mm F3.5 macro lens mounted on telescoping extension tube and flash. Kodachrome 64 film. Photo by Joe Warfel.

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1996. The Journal of Arachnology 24:173–185

INITIAL TESTS FOR PRIORITY EFFECTS AMONG SPIDERS THAT CO-OCCUR ON SAGEBRUSH SHRUBS

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ABSTRACT. Recent work in conservation biology and restoration ecology has highlighted the need for research on the process of community assembly and the effect of initial conditions on community development. Theory and limited experimental work in this area suggest that an initial "pioneer" colonist arriving in open habitat can strongly influence this process, resulting in a priority effect. We used a ubiquitous terrestrial animal group, spiders, to test for the existence of priority effects during colonization of individual sagebrush shrubs. In 1992, at a site in northern Utah, we applied three treatments to subsets of 60 cleared shrubs that represented available habitat to spiders. Two shrub treatments received different jumping spider pioneer colonists placed by hand (either *Metaphidippus aeneolus* (Curtis 1892) or *Phidippus johnsoni* (Peckham & Peckham 1883)), and a third shrub treatment received no placed spiders, serving as a reference. After 3–4 days of exposure to the same environmental conditions, including natural colonization by dispersing spiders, we collected a total of 285 spider assemblages that had developed on shrubs. We compared these assemblages by treatment type at both the species and guild levels, defining spider guilds based on differences in morphology and foraging technique (e.g., jumpers, trappers, ambushers, and pursuers).

The total number of spiders per shrub was not significantly different by treatment type ($P = 0.279$), and overall measures of species richness and abundance were similar. At the guild level of analysis, however, differences were observed. Total counts of trappers were 43–50% lower in treatments receiving a placed jumper pioneer. A log-linear model comparing treatments as a whole confirmed that jumper pioneers significantly reduced trapper numbers in subsequent assemblages compared to those from reference shrubs ($P = 0.019$), and significantly fewer trappers were collected from shrubs that had *Metaphidippus aeneolus* as a pioneer ($P = 0.034$). This evidence of short-term priority effects was found despite a conservative aspect of our test, in which the reference shrubs had some likelihood (35%) of receiving either of these jumper pioneers by chance from natural dispersal. It is not known whether these priority effects persist over longer time scales.

The observed results are consistent with predictions based on known spider behaviors of cannibalism and interguild predation. Outcomes of these spider-spider interactions relate to differences in foraging technique and body size. We suggest that a guild-level approach and the shrub-spider system we describe have promise for future research on priority effects and animal community assembly.

A major focus of research in animal ecology has been understanding how extant natural communities maintain their structures over time through such mechanisms as competition and predation (see reviews in Strong et al. 1984; Diamond & Case 1986; Kikkawa & Anderson 1986; Gee & Giller 1987; but also Dunson & Travis 1991). But contemporary problems in conservation biology and ecosystem restoration (Bradshaw 1987; Cairns 1988; Buckley 1989; Soule & Kohm 1989; Hansson 1992) have challenged us to expand this program, both by considering how animal communities change over time (Pimm 1986, 1991; Giller & Gee 1987; Lawton 1987; Crawley 1989; Luken 1990) and by analyzing disturbed systems (Lewontin 1969; Sousa 1984; Pickett & White 1985; Harper 1987). In short, we are starting to pay more attention to the process of community development itself, exploring the sensitivity of ecological systems to different initial conditions and tracking community trajectories over time (Connor & Simberloff 1979; Fox 1987; Gilpin 1987; Drake 1990a, 1990b, 1991; Drake et al. 1993; Law & Morton 1993). The promise of this approach lies in the potential to describe particular "assembly rules" for natural commu-

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nities (M'Closkey 1978, 1985; Haefner 1981, 1988; Fox & Kirkland 1992; Fox & Brown 1993; Luh & Pimm 1993; Grover 1994) and relate them to problems in applied ecology. In a sense, this would fulfill Robert MacArthur's vision that ecological research would eventually yield a series of empirical rules in the form: "for organisms of type A, in environments of structure B, such and such relations will hold" (MacArthur 1972).

To some ecologists, these endeavors recall decades-old disputes concerning the existence of communities, the analysis of species co-occurrence data, and the description of species assembly rules (e.g., Wilson 1991, 1994, 1995; see responses by Palmer & White 1994; Fox & Brown 1995). Fox & Brown (1995) restate an important distinction between most earlier work and recent efforts in that guilds rather than species are often used to characterize assembly rules (M'Closkey 1978, 1985; Haefner 1981; Fox & Kirkland 1992; Fox & Brown 1993). Species are assigned to guilds based on ecological roles or functional similarities that not only simplify the number of variables but may also facilitate comparative studies and lead to broader utility. Although part of a continuum, we also note that manipulative studies of assembly rules are often concerned with short time scales between colonization events (days to years, see comments by Grover & Lawton 1994) and smaller spatial scales than biogeographic or animal succession studies (e.g., Morton et al. 1994; Shenbrot et al. 1994; Kelt et al. 1995).

A subset of assembly rule theory concerns the influence of an initial, "pioneer" colonist on subsequent community development (Drake 1990a). In replicated trials, if the identity of the pioneer changes the community trajectory and results in different community patterns at some later time, a "priority effect" is said to have occurred (Drake 1990a). In such cases, it is not only the community components that affect structure, but also the sequence of their interactions. One implication for applied ecology is that a "saving all the parts" strategy may be inadequate for ecosystem restoration if historical information is not considered (Drake 1990a; Luh & Pimm 1993). To date, studies of priority effects within animal communities have been performed under highly-controlled laboratory conditions with algae and protozoans (Dickerson & Robinson 1985; Gilpin et al. 1986; Robinson & Dickerson 1987; Robinson & Edgemon 1988; Drake 1991; Drake et al. 1993), and under field conditions with sessile invertebrates (Dean & Hurd 1980), dipterans (Kneidel 1983), ants (Cole 1983a, 1983b), odonates (Morin 1984), and frogs (Wilbur & Alford 1985).

Here, we report on the detection of short-term priority effects, in the field, among spiders (Arachnida, Araneae) that colonize shrub-steppe habitat in northern Utah. We believe this system has significant advantages for addressing assembly rule questions. Spiders are ubiquitous terrestrial animals and, as generalist predators, they have been model organisms for many ecological studies (Barnes 1953; Turnbull 1973; Foelix 1982; Spiller & Schoener 1988, 1990; Wise 1993). Spiders are also taxonomically diverse, locally abundant, and easy to manipulate. The shrub-steppe habitat type is globally widespread and individual shrubs represent habitat "islands" (*sensu* Price 1984) for many arid-land spiders (Fautin 1946; Chew 1961; Abraham 1983). Shrubs help spiders reduce some environmental stresses while providing substrates that facilitate prey capture (Hatley & MacMahon 1980; Riechert & Gillespie 1986). In northern Utah, Abraham (1980, 1983) reported that the spider faunae on big sagebrush shrubs (*Artemisia tridentata* Nutt.) shrubs are distinctive when compared to the local ground and herb stratum faunae. This observation, coupled with evidence that individual spiders remain on the same shrub for days to weeks (Wing 1984), suggests to us that, to some extent, individual shrubs define discrete spider assemblages and may be used as experimental units. Other studies with invertebrates have also adopted this perspective (see Price 1984).

The spider assemblages that develop in a given area are a consequence of dispersal processes (both ground and aerial mechanisms, see Turnbull 1973; Foelix 1982; Decae 1987; Greenstone 1990; Crawford et al. 1995) and interactions among colonists and their environment. In sagebrush shrub habitat in Utah, previous workers have studied the influences of substrate type, vegetation architecture, prey availability and dispersal mechanism on spider community structure (Hatley & MacMahon 1980; Robinson 1981, 1984; Abraham 1983; Wing 1984; Ehmann 1994a, 1994b). In

this study, we attempt to control or randomize these variables to detect priority effects among spiders that co-occur on sagebrush shrubs.

Spider assemblages can be described at both the species and guild levels of organization. Although the guild concept introduced by Root (1967) has been the subject of some confusion and debate (Hawkins & MacMahon 1989; Simberloff & Daylan 1991), it has value when organisms are grouped in biologically appropriate ways to study complex systems (MacMahon 1976; Hawkins & MacMahon 1989). This approach also has statistical utility, particularly when counts of individuals within species categories are low. In this study, we classified spider species into four *a priori* guilds based on behavioral observations of their foraging techniques and taxonomic characteristics at the family level, following Hatley & MacMahon (1980) and Wing (1984). "Jumpers" (including Oxyopidae and Salticidae of this study) are active, visually-oriented predators that leap onto their prey (Foelix 1982). "Trappers" (including Araneidae, Dictynidae, Linyphiidae, and Theridiidae) are sit-and-wait predators that rely on silk constructions to capture prey (Gertsch 1979). "Ambushers" (including Thomisidae) are sit-and-wait predators that require direct contact with prey for capture, and their first two pairs of legs are commonly elongated (Gertsch 1979; Wing 1984). "Pursuers" (including Anyphaenidae, Clubionidae, and Philodromidae) actively chase and overtake prey along the substrate using four pairs of subequal length legs (Kaston 1978).

The existence of priority effects among spiders on individual shrubs depends on the occurrence of significant spider-spider interactions, which must involve positive and/or negative components. Positive interactions are primarily known from studies of communal webs in tropical environments (Uetz 1986; Uetz & Hodge 1990); whereas, in temperate environments, four lines of evidence suggest that negative interactions predominate. First, cannibalism is widespread among spiders and it has been suggested that the major enemies of spiders are spiders themselves (Bristowe 1941; Foelix 1982; Wise 1993). Cannibalism not only provides a spider with a meal but eliminates a conspecific who is a potential competitor, a behavior that is expected to enhance lifetime fitness (see discussions in Elgar & Crespi 1992; Crowley & Hopper 1994). Second, spiders and their scorpion relatives are known to participate in intraguild predation, wherein different species of the same functional group feed upon each other (Schaefer 1972 as cited by Wise 1993; Polis & McCormick 1987; Polis et al. 1989; Hurd & Eisenburg 1990). Third, although many spider families remain unstudied (Wise 1993), there is experimental evidence for interspecific competition among two orb-web spiders (Araneidae) (Spiller 1984a, 1984b, 1986). Finally, non-random web spacing patterns observed for some arid-land spiders suggest that spiders are territorial (Riechert et al. 1973; Riechert 1981). In northern Utah, several workers have observed that cannibalism, intraguild predation, and interguild predation occur among shrub-dwelling spiders (Abraham 1980; Wing 1984; this study, see Discussion).

Our test for priority effects among shrub-dwelling spiders involved three experimental treatments applied to subsets of 60 shrubs (yielding a total of 285 samples) during the summer of 1992, and indicates that short-term priority effects occur at the guild level of organization. The results are consistent with known spider-spider interactions related to differences in foraging technique and body size.

METHODS

Spiders.—Previous sampling during two summers indicated that several jumping spiders among the 41 spider species identified on Mill Hollow shrubs were much more common than others, which suggested their use as experimental pioneer colonists. These spiders, *Metaphidippus aeneolus* (Curtis 1892) and *Phidippus johnsoni* (Peckham & Peckham 1883), represented 25% and 21% respectively of the spider fauna sampled from 769 census shrubs on the same plot during 1990–1991, and at least one of these species was present on 70% of the 325 census shrubs sampled in the year of this study (1992). Their abundance gave us a practical advantage in facilitating their collection for the experiment, but these species were also desirable because it is likely that they are common pioneer colonists at Mill Hollow. In addition, behavioral observations of jumping spiders, which are active and versatile hunters (Foelix 1982; Forster 1982), led

us to expect that they would be involved in the strongest spider-spider interactions that might result in priority effects. These spiders are also large enough (adult body lengths 7–12 mm) to be easily manipulated, marked, and released. Voucher specimens of this study have been deposited at the Field Museum, Chicago, Illinois.

Shrubs.—The site chosen for this research lies at the eastern edge of the Great Basin shrub-steppe ecosystem in Mill Hollow, Cache County, Utah (see Ehmann 1994a for details). A rectangular grid measuring 50 m × 120 m and containing approximately 1200 shrubs, was divided into 60 cells (each containing 10 m^2). Within each grid cell, one shrub was selected as a sampling unit for collecting spider assemblages. The grid ensured that, on average, experimental shrubs would be at least 10 m apart, which we felt was large relative to observed spider movement distances (a jumper, *Phidippus johnsoni*, 2 m in one day (Ehmann, pers. obs.); an ambusher, *Misumena vatia* (Clerck 1757), 0.24–0.55 m/day (Morse 1981; Morse & Fritz 1982)). Our second criterion for shrub selection was shrub size, which we wanted to hold as constant as possible. In particular, we wanted to limit variation in canopy size, both to standardize the likelihood of aerial colonization and the amount of available substrate for spiders (Hatley & MacMahon 1980; Robinson 1981; Abraham 1983; Wing 1984). We measured candidate shrubs for maximum canopy width (MCW), canopy width perpendicular to maximum canopy width (PCW), and mean canopy height (MCH). We also required shrubs to have a single trunk at ground level (for equivalent ground colonization opportunities by spiders) not be in above-ground contact with any adjacent shrub, and be spaced at least two shrubs away from any other experimental shrub. In general, we sought shrubs that were approximately 50 cm in both width measurements and approximately 75 cm in average height. However, sagebrush has a variable growth form and we had the added complication of a small field site and a limited number of shrubs/grid cell to choose from. Consequently, some variation in shrub size persisted after final selection (Table 1), although all three measured variables formed normal distributions with no significant skewness or kurtosis ($P > 0.05$, two-sided t-tests, Sokal & Rohlf 1981).

Table 1.—Summary of descriptive statistics for 60 sagebrush shrubs selected for this study (MCW = maximum canopy width, PCW = canopy width perpendicular to MCW, MCH = mean canopy height). All three variables are normally distributed.

	Shrub measurement (cm)		
	MCW	PCW	MCH
Mean	69.5	51.2	47.3
Standard deviation	13.5	10.5	7.6
Minimum	45.0	36.0	31.0
Maximum	100.0	90.0	72.0
Median	66.0	49.5	47.0
Skewness	0.76	1.21	0.62
Kurtosis	−0.34	1.95	1.00

Field trials.—To set up each field trial, a random subset of the 60 experimental shrubs was cleared of spiders using a variation on a beating-sheet technique (Southwood 1978). At the Mill Hollow site, striking a shrub (of the size detailed above) with an axe handle 30 times in approximately 15 sec yields, on average, 86% of the total number of spiders present on the shrub (Ehmann 1994a). To achieve a higher rate, consistent with the goals of this study, we added a second beating episode, at least 30 min following the first beating, to collect the residual spiders. A field trial with 10 shrubs verified a 100% collection rate using this double-beating method, and it was adopted for this study. Other concerns about induced leaf loss from shrubs, spider detection in the litter, and variation in spider abundance with sampling intensity were allayed with other preliminary tests (see Ehmann 1994a). Spiders collected from shrubs were removed from the grid cell.

Cleared shrubs were randomly assigned one of three experimental treatments: those that received a *Metaphidippus aeneolus* individual as a pioneer colonist (Treatment 1), those that received a *Phidippus johnsoni* individual (Treatment 2), and those that did not receive a placed spider ("reference shrubs", Treatment 3). Spiders used for release were typically late instar immatures collected from sagebrush shrubs adjacent to the field site. They were released onto cleared shrubs from a vial placed along the shrub trunk halfway between the canopy and the ground. After

treatment, 3–4 days were allowed for subsequent colonization by spiders and the developed assemblages were collected using the double-beating technique described earlier. Sampled shrubs are quickly recolonized (often within 24 h to average densities), and those without any spiders are uncommon (11% of 1094 shrubs sampled from 1990 to 1992). Although spider colonization is a continuous process, we were most interested in the assemblages that developed shortly after pioneer arrival. Collections were only performed in the absence of wind.

Seven experimental trials were performed from 19 July–18 September 1992, about one week apart. In the first six trials, 15 shrubs/treatment were used and in the seventh trial only five shrubs/treatment were used (due to a scheduling limitation), yielding a total of 285 sampled shrubs for the experiment. Data from one Treatment 2 shrub were lost.

Shrub selection.—To minimize the effect of remaining shrub size variation and other uncontrolled variables (e.g., prey density, microclimate), we randomized shrub selection and treatment assignment for each trial. This randomization assured good interspersion of treatments (Hurlbert 1984), but also meant that any shrub (of the 60 measured and set aside for this experiment) might be assigned to any of the three experimental treatments for a given trial, or remain unused. With more uniform shrubs, a strict repeated measures design would be appropriate, but we were limited to a small site with a small number of similar shrubs. Four considerations suggest that our imposition of treatments was acceptable and our observations from these shrubs were essentially independent. First, we detected no significant changes in physical shrub characteristics from one trial to the next due to sampling. We have previously referred to insignificant differences in leaf loss and spider abundance under different sampling regimes, and observed no other differences in shrub or site condition due to sampling. We did not measure chemical components of shrubs or chemicals that may have derived from spider activity, however, Wiens et al. (1991) reported no significant association of spider numbers with variation in sagebrush shrub chemicals. Second, all treatment shrubs were cleared of spiders before use, and at the end of each trial, all spider colonists were permanently removed. Third, it seems highly unlikely that newly colonizing spiders would have any influential previous experience with the shrubs selected for a given trial, which were widely-spaced relative to on-site movements of the study organism. Fourth, in this prefatory work, we did not seek to predict particular spider assemblages on particular shrubs, but rather to compare average patterns among three treatments. Assignment of shrubs to treatments was equally random for each trial, "averaging out" uncontrolled differences. These details suggest to us that no significant carry-over effects occurred from one trial to the next, and that the treatments can be validly compared. We believe larger concerns would have arisen from steady use of atypical shrubs at our site, which could have resulted from a single randomization of treatment assignments and a repeated measures design.

Statistical analysis.—To compare treatments, we calculated species level comparisons of richness and abundance among treatments using the BASIC program SPDIVERS (Ludwig & Reynolds 1988) based on definitions by Hill (1973) and Alatalo (1981). We also compared the total number of spiders/shrub/treatment using contingency table analysis (Sokal & Rohlf 1981). Finally, counts of spiders in each guild by treatment type were compiled. These formed highly-skewed frequency distributions that resisted transformations for homoscedasticity and normality required for standard analysis of variance (ANOVA) tests. The limited number of categories for some guild counts reduced the value of contingency table analysis (except when the comparison between total spiders per shrub and treatment type was made), and nonparametric tests would have resulted in a substantial loss of information. For these reasons, we chose to analyze guild-level data using standard log-linear modeling techniques, which do not require ANOVA assumptions or large counts, and do not reduce information.

Log-linear models are a subset of generalized linear models which also include well-known ANOVA and linear regression techniques (McCullagh & Nelder 1983). To fit a log-linear model, it is first assumed that the data reflect independent observations (see earlier comments). Second, an underlying distribution (which does not have to be a normal distribution) is adopted for the model. Based

on goodness of fit tests using the guild counts per shrub by treatment, a Poisson distribution was accepted ($P > 0.05$).

The model was designed to predict the number of spiders within each guild among different shrub treatments over time. For each guild a two-way table was constructed with three levels (rows) for treatment and seven levels (columns) for time. Observed counts of spiders were assigned to the appropriate cells (15 counts/cell for six columns (one had 14), and 5 counts/cell for the seventh column). The full model asserts that counts within each cell can be expressed as a linear combination of date effects, treatment effects, and an interaction of date and treatment effects, and can be written as:

$$\log \mu_{ij} = \mu + \text{treatment}_i + \text{date}_j + (\text{treatment} \times \text{date})_{ij}.$$

Four subsets of this model were also fit to the data: a null model which states that there is no effect by treatment, date, or treatment × date interaction, a model that assumes only a date effect, a model that assumes only a treatment effect, and a model that assumes only treatment and date effects (no interaction). The GLM procedure in the S-PLUS statistical package (Statistical Sciences, Inc., Seattle, Washington) was used to fit these five models to the data in each of the four guild tables (date was used as a blocking factor and fit first). No significant treatment × date interaction was detected ($P > 0.05$) and this term was removed from the full model. A 5% level of significance was selected for interpretation.

RESULTS

A total of 570 spiders was collected during the experiment (Table 2), representing a minimum of 26 species (95.8% of the spiders were identified to species level, 3.7% were identified to guild level, and 0.5% remained unidentified). Due to the short time frame considered in this experiment (to detect early priority effects), the average number of spiders per shrub was small (2 spiders/shrub, but note range of 0–14), but again, we sought mainly to compare groups of shrubs treated the same way, not single shrubs. At the species level, *Sassacus papenhoei* (Peckham & Peckham 1895) and *Hyposinga singaeformis* (Scheffer 1904) numbers were especially reduced on shrubs with placed jumpers. On shrubs with placed *Phidippus johnsoni*, *Misumenops* sp. was more frequently collected and *Anyphaena pacifica* (Banks 1896) was less frequently collected relative to the two other treatments. All three treatments appear similar in terms of Hill's (1973) indices for overall species richness and species abundance (Table 2). The total number of spiders per shrub was independent of treatment type (Table 3, $X^2 = 12.096$, $df = 10$, $P = 0.279$).

At the guild level, inspection of the data reveals that shrub treatments with placed jumping spiders had 43–50% fewer trappers and 28–40% more pursuers relative to the reference treatment (Table 2). The log-linear model indicated two significant differences (Table 4). First, comparisons based on four different treatment combinations revealed that significantly fewer trappers were collected from shrubs that had *Metaphidippus aeneolus* as a pioneer compared to reference shrubs (Treatment 1 vs. Treatment 3, $P = 0.034$). Second, there were significantly fewer trappers collected from shrubs that had either jumper as a pioneer compared to reference shrubs (Treatments 1 and 2 combined vs. Treatment 3, $P = 0.019$). Tests with the model involving other guilds and comparisons were not significant at $P = 0.05$.

DISCUSSION

In a manipulative field experiment, *Metaphidippus aeneolus* pioneers significantly reduced trapper numbers in subsequent spider assemblages ($P = 0.034$), indicating that a priority effect occurred. *Phidippus johnsoni* pioneers did not yield a significant result, although the raw count data differs by only two trappers (Table 2). When treatments were combined for analysis, jumpers also significantly reduced trapper numbers ($P = 0.019$). This short-term response was detected despite some likelihood (35%) that cleared reference shrubs would have received one of these same jumper pioneers simply by chance (and a 66% chance of receiving any jumper species, based on 1992 census data). In this sense, our test was somewhat conservative. This detail may be balanced by the observation of only two significant results at the 0.05 level among 16 tests performed (4 comparisons × 4 guilds). If a severe correction is made for these multiple comparisons (e.g., Bonferroni test), the results of the log-linear model are not signif-

Table 2.—Counts of spiders collected from experimental shrubs (19 July–18 September 1992) arranged by guild and species identity for three treatments (*Metaphidippus aeneolus* = Treatment 1, *Phidippus johnsoni* = Treatment 2, reference = Treatment 3), accompanied by Hill's (1973) indices for species richness and diversity (N0 = species richness, N1 = number of abundant species, N2 = number of very abundant species).

	Number of spiders		
Identity	*M. aeneolus*	*P. johnsoni*	Reference
Jumpers			
Metaphidippus aeneolus (Curtis 1892)	54	32	24
Oxyopes scalaris (Hentz 1845)	6	6	2
Habronattus hirsutus (Peckham & Peckham 1888)	2	5	5
Phidippus johnsoni (Peckham & Peckham 1883)	29	44	31
Phidippus sp.	0	2	0
Sassacus papenhoei (Peckham & Peckham 1895)	26	35	48
Synageles idahoanus (Gertsch 1934)	4	2	6
Tutelina similis (Banks 1895)	4	5	3
Unidentified	3	2	2
Guild total	128	133	121
Trappers			
Dictyna idahoana (Chamberlin & Ivie 1933)	1	0	0
Dipoena nigra (Emerton 1882)	0	0	1
Dipoena tibialis Banks 1906	4	5	9
Erigone sp.	0	1	0
Euryopis sp.	1	0	3
Hyposinga singaeformis (Scheffer 1904)	2	2	9
Metepeira foxi (Gertsch & Ivie 1936)	2	2	1
Theridion neomexicanum Banks 1901	3	3	1
Unidentified	1	3	4
Guild total	14	16	28
Ambushers			
Coriarachne sp.	1	0	0
Misumena vatia (Clerck 1757)	0	1	0
Misumenops sp.	1	7	2
Xysticus gulosus Keyserling 1880	5	1	5
Xysticus montanensis Keyserling 1887	1	0	0
Xysticus sp.	2	3	4
Unidentified	1	1	0
Guild total	11	13	11
Pursuers			
Anyphaena pacifica (Banks 1896)	8	1	6
Chiracanthium inclusum (Hentz 1847)	7	12	5
Philodromus histrio (Latreille 1819)	12	14	8
Thanatus formicinus (Clerck 1757)	2	4	3
Tibellus oblongus (Walckanaer 1802)	1	3	2
Unidentified	2	1	1
Guild total	32	35	25
Unidentified	2	0	1
Total spiders collected (n = 570)	187	197	186
Total number of shrubs (n = 284)	95	94	95
Species richness (N0)	21	20	19
Number of abundant species (N1)	9.9	9.9	10.4
Number of very abundant species (N2)	6.5	7.1	7.2

Table 3.—Summary of contingency table analysis of total number of spiders per shrub. Frequencies represent the number of shrubs within each treatment. The three largest contributions to the chi-square value are marked (+). $\chi^2 = 12.096$, $df = 10$, $P = 0.279$.

	Observed frequencies Shrub treatment			Expected frequencies Shrub treatment		
Total spiders	*M. aeneolus*	*P. johnsoni*	Reference	*M. aeneolus*	*P. johnsoni*	Reference
0	19	13	20	17.39	17.21	17.39
1	30	25	28	27.76	27.47	27.76
2	20	28+	13+	20.41	20.19	20.41
3	11	13	21+	15.05	14.89	15.05
4	8	9	6	7.69	7.61	7.69
≥5	7	6	7	6.69	6.62	6.69
Total	95	94	95	95.00	94.00	95.00

icant. We note, however, that the log-linear model results are internally consistent, parallel other results from our study in a highly suggestive way, and match other published reports of spider-spider interactions.

We observed that when a jumping spider is placed onto a new shrub, the spider is usually very active and begins a nearly comprehensive exploration of the shrub branches and canopy (see also Wing 1984). Once these movements are performed, a pioneer may be familiar enough with its surroundings to detect quickly new arrivals. Salticids have extremely good eyesight for distances up to 40 cm (Foelix 1982), and may effectively survey the ~70 cm diameter shrubs used in this study. As trappers also perform some exploration of the shrub prior to web-site selection (Riechert & Gillespie 1986), their movements following colonization may be readily detected by active visual predators such as jumpers (even at night, see Forster 1982). Extended activity associated with web construction may further enhance their detection by jumpers, and the chemical properties of the silk itself may act as stimuli to other spiders (Tietjen & Rovner 1982; Pollard et al. 1987). Completing a web before a jumper arrives may not eliminate this threat, as Jackson (1977) and Robinson & Valerio (1977) report that jumpers capture trappers on webs.

As noted earlier, spiders are often the major predators of other spiders. The outcome of an attack is usually a function of body size, with the smaller spider becoming the victim (Hallander 1970; Nentwig 1987; Dong & Polis 1992). As the smallest spiders at the site, trappers may be especially vulnerable to interguild predation. During this study, we observed *Metaphidippus aeneolus* attacks on a trapper (*Metepeira foxi* (Gerstch & Ivie 1936)); and Morse (1992) has described *Metaphidippus* predation on an ambusher (*Misumena*). *Phidippus johnsoni* is known to prey heavily on spiders, including trappers such as Theridiidae and Dictynidae (both present at Mill Hollow) (Jackson 1977). *P. johnsoni* usually attacks prey that measures 25–75% of its own body size (Jackson 1977), and nearly all Mill Hollow trappers lie within this range for late-instars and adults. We also observed immature *Phidippus johnsoni* capturing an am-

Table 4.—Summary of results from comparisons performed with a log-linear model to detect guild-level differences among three shrub treatments (Treatment 1 = *Metaphidippus aeneolus* pioneer; Treatment 2 = *Phidippus johnsoni* pioneer; Treatment 3 = reference).

Treatment comparison	Result	*t*	*df*	*P*-value
1 vs. 3	Fewer trappers if *M. aeneolus* is pioneer	−2.126	275	0.034
2 vs. 3	No significant differences			
1 and 2 vs. 3	Fewer trappers if a jumper is pioneer	−2.360	276	0.019
1 vs. 2	No significant differences			

busher (*Xysticus* sp.). Cutler et al. (1977) documented another jumper, *Oxyopes scalaris* (Hentz 1845), capturing members of five spider families, including trappers.

Pursuers were found in greater numbers in both jumping spider treatments relative to the reference treatment, though these differences were not statistically significant. These two groups are the most similar in adult body size, which may reduce stimuli for interguild predation and favor coexistence. Also, even if a jumper is approached by a pursuer, it may avoid capture by a single jump, a movement the pursuer cannot perform.

Intraguild predation was also observed among jumpers at our site, including cannibalism by *Metaphidippus aeneolus* and 11 attacks by immature *Phidippus johnsoni* on other immature spiders including four jumpers (conspecifics, *M. aeneolus*, *Sassacus papenhoei*, *Habronattus hirsutus* (Peckham & Peckham 1888)). Cutler (1991) has also reported predation by *Phidippus* on immature conspecifics. We also recorded adult *S. papenhoei* predation on immature *P. johnsoni*, an immature *S. papenhoei* preying on immature *M. aeneolus*, and an adult *Oxyopes scalaris* preying on immature *M. aeneolus*.

In all cases that we observed, the larger (attacking) spider consumed the smaller spider. Shrub spiders likely share similar environmental requirements, and given the demands of life in an arid climate, may be "enemies doomed to associate" (Diamond 1992). Other spiders may be some of the most available and reliably caught prey that they encounter on shrubs, and these interactions can be expected to directly influence spider assemblage structure.

Because *Metaphidippus aeneolus* and *Phidippus johnsoni* are members of the same guild, our tests have some relevance to recent discussions concerning the extent of species redundancy in nature (Walker 1992; Lawton & Brown 1993; Morin 1995). In our tests, only one statistically significant difference between these two species was detected. Because of the high species richness of spiders found among sagebrush shrubs and the high relative abundance of jumpers, we suggest that this system is well-suited for new experimentation on this question.

Finally, Moran & Hurd (1994) have described predator avoidance behavior by spiders in response to introductions of mantids. Spider emigrations occurred rapidly after mantid introduction, especially among smaller size classes. Whether shrub spiders respond in a similar manner to other spiders is not known. Although we cannot exclude this mechanism, our present interpretations are based on widely-reported phenomena of cannibalism and interguild predation among spiders.

CONCLUSIONS

We have described a system and an experimental approach that we believe has value for work on assembly rule theory, in which community components can be manipulated and added to discrete habitat units in different temporal sequences. In preliminary experiments with two different jumper pioneer treatments, trapper numbers were reduced compared to a reference treatment, indicating that a priority effect occurred. Although we are unable to eliminate all ambiguity, we infer that spider-spider interactions can explain these outcomes, based on differences in foraging technique and body size. It is not known how long the observed priority effects persist or what the outcomes would be if trappers or other spiders were the pioneer colonists. We believe that additional work in this system, already underway, can test ideas concerning models of animal community assembly.

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PATTERN AND DURATION OF COPULATION IN WOLF SPIDERS (ARANEAE, LYCOSIDAE)

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ABSTRACT. The temporal patterns of insertion of male palps, expansion of the hematodocha and duration of copulation are reported for 10 species of *Schizocosa* Chamberlin 1904, three species of *Rabidosa* Roewer 1955, one species of *Gladicosa* Brady 1986, one species of *Hogna* Simon 1885, two species of *Isohogna* Roewer 1960, one species of *Trochosa* C.L. Koch 1848, one species of *Geolycosa* Montgomery 1904, two species of *Arctosa* C.L. Koch 1848, three species of *Alopecosa* Simon 1885 and six species of *Pardosa* C.L. Koch 1847. In all species of *Schizocosa* examined so far, males showed a pattern composed of a series of insertions with one palp followed by a switch to the opposite side and a separate series of insertions with the other palp. During each insertion there was a single expansion of the hematodocha. These copulations generally lasted from 1–4 hours. Males of *Gladicosa bellamyi* (Gertsch & Wallace 1937) and *Hogna georgicola* (Walckenaer 1837) likewise showed a series of insertions on one side followed by insertions on the other side, with a single expansion of the hematodocha with each insertion. Males of *Arctosa littoralis* (Hentz 1844), *A. sanctaerosae* Gertsch & Wallace 1935 and *Geolycosa rogersi* Wallace 1942 each copulated by alternating palps with a single insertion and single expansion of the hematodocha. The alternating pattern of insertions was also seen in *Rabidosa rabida* (Walckenaer 1837), *R. hentzi* (Banks 1904) and *R. punctulata* (Hentz 1844). *Isohogna lenta* (Hentz 1844) (a single individual) alternated between multiple expansions of the hematodocha during one insertion and alternating sides with a single insertion and expansion per side. A second member of *Isohogna* showed a single insertion on one side with multiple expansions of the hematodocha. Comparisons with published descriptions of copulatory pattern suggest that *Schizocosa* and *Trochosa* Koch 1848 may form a monophyletic clade in the "*Trochosa* group" of the Lycosinae. The copulations that involved multiple insertions of the male's palp on one side with a single expansion per insertion were long copulations (1–4 hours). This may provide for multiple opportunities of *in copula* courtship. *Arctosa* copulations were very short (18–46 sec), while the *Geolycosa* copulations were relatively short (5–7 min). Thus, the copulations of the burrowing spiders were much shorter than the nonburrowing spiders.

Copulatory behavior in spiders has long fascinated arachnologists (Clerck 1757 in Kaston 1936; Montgomery 1903, 1909; Bristowe 1926; Gerhardt & Kaestner 1937; Savory 1928; other references in Bonnet 1945; Robinson 1982) partly because there is an impressive array of copulatory positions and patterns. Also, in spiders, the potential for sexual cannibalism exists (Arnqvist 1992; reviewed in Elgar 1992), strongly reinforcing the need for clear communication both before and during copulation. Although there have been numerous studies on copulatory behavior in a variety of spiders, relatively few have focused on the patterns of insertion of the male palp during copulation in the Lycosidae (Engelhart 1964; Rovner 1973, 1974; Costa & Sotelo 1994). We here present the patterns of palpal insertion, hematodochal expansion and duration of copulation seen in numerous lycosid species. We also present the first attempt to look at these behaviors in spiders in a phylogenetic context.

In wolf spiders (Lycosidae), the male mounts the female so that they face opposite directions, and the ventral surface of the anterior portion of the male's prosoma is against

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the dorsal surface of the female's abdomen. The relative positions of males and females *in copula* were described by Gerhardt & Kaestner (1937) who categorized five different copulatory positions for spiders. The position described for wolf spiders (above) is also seen in pisaurid genera *Thalassius* Simon 1885 (Sierwald 1988), *Dolomedes* Latreille 1804 (Arnqvist 1992), and *Pisaurina* Simon 1898 (Bruce & Carico 1988) and Agelenidae (Fraser 1986; Gering 1953; Foelix 1982), as well as most "advanced" wandering spiders, including Philodromidae, Clubionidae and Salticidae (Foelix 1982). The *Pisaurina* shows the same position, but with both spiders hanging from a silken thread during copulation.

Once mounted, the lycosid male touches the anterior end of the female's abdomen, causing her to rotate the abdomen. He then scrapes the side of the female's abdomen with his palp, and most times the palp engages with the epigynum apparently by the median apophysis of the palp catching on the epigynal hood (unpubl. data, based on examination of high magnification videorecording from the ventral aspect of *Schizocosa* sp. nr. *crassipes* [Walckenaer 1837]). The right palp engages with the right side of the epigynum; the left palp engages the left side. Once engaged, the male expands the hematodocha which causes the embolus to coil into the female's copulatory duct and at some point, sperm is transferred. The timing of sperm transfer in groups with multiple insertions or with multiple hematodochal inflations has never been determined for any species. We call the physical act of the coupling of the male palp with the female epigynum an "insertion". The hematodocha may expand one or more times during a single insertion. If the male spider inserts the same palp multiple times before switching sides, a "series" of insertions or "multiple insertions" occurs (Rovner 1974).

Behavior has provided useful characters in the phylogenetic studies of the Lycosoidea clade. Carico (1986, 1993) looked at method of egg sac transport, structure of egg sac seam, method of maternal care, silking of female during copulation, the structure of the web retreat, reattachment of the egg sac, as well as the structure of the nursery web. Merrett (1988) used several behavioral traits in placing *Ancylometes bogotensis* (Keyserling 1876) in the Pisauridae. Griswold (1993) used two behavioral characters (nursery web and method of egg sac transport) in his phylogenetic analysis of Lycosoidea. Copulatory pattern has not yet been used in phylogenetic contructions as it has been reported only for a few species outside of the Lycosidae.

In 1973, Rovner suggested that Gertsch & Wallace's (1937) placement of *Schizocosa avida* (Walckenaer 1837) into the genus *Schizocosa* was supported by the copulatory pattern demonstrated by that species (Rovner 1973). Rovner noted that the pattern of palpal insertions in *Rabidosa rabida* was qualitatively distinct from the patterns demonstrated by *Schizocosa*, particularly *S. saltatrix* (Hentz 1844) observed by Rovner (1972) and *S. bilineata* (Emerton 1885) and *S. ocreata* (Hentz 1844) observed by Montgomery (1903). This was the first time copulatory behavior was used to investigate taxonomic placement in *Schizocosa*. Costa & Sotelo (1994) provided a brief review of copulatory patterns in wolf spiders and suggested that generally there are few differences in copulatory patterns among closely related species, but the differences become more notable at higher taxonomic levels.

We here report on the patterns of palpal insertion, hematodochal expansion, and copulation duration that we have observed in 10 species of *Schizocosa*. For many of these, we have observed copulatory behavior in several populations from a wide geographic range. We also report on the copulatory pattern seen in eight other North American lycosid species representing five genera. Additional data are provided for *Pardosa*, *Hogna*, *Geolycosa* (Dondale & Redner unpubl. data), for *Sosippus* Simon 1888 (Rovner unpubl. data) and for *Alopecosa* and *Hygrolycosa* Dahl 1908 (Kronestedt 1979, unpubl. data) and are discussed in the context of our observations. While this is still a relatively small proportion of the 2200 species of wolf spiders that exist worldwide (Coddington & Levi 1991), the patterns observed so far warrant some discussion. We also hope this report may stimulate other researchers to examine more species of lycosids for patterns in copulatory behavior.

METHODS

Wolf spiders were collected throughout the southeastern USA during the spring, summer and fall of 1993, 1994, 1995 and in the spring of 1996. Immature and mature individuals

were returned to the laboratory at the University of Mississippi where they were individually maintained in vials (8.5 cm × 5 cm) with wicks that extended into a water tray providing a constant source of moisture. Appropriately sized crickets were offered twice weekly as food for the spiders. Temperature in the laboratory ranged from 22–25 °C. Temperature during copulation was 22–25 °C. Spiders were kept on an L:D schedule of 14:10. Animals were only used once in a courtship/copulation observation and were generally used a few days to a few weeks after collection.

Courtship and copulation were observed for most species by setting the female in a culture dish with a piece of filter paper 6–12 hours before observations. Males and females were then placed with the filter paper in an observation chamber where their interactions were videotaped using a Panasonic HD-5000 videocamera with a 105mm Macrolens. *Arctosa* species and *Geolycosa rogersi* were observed by placing the female in a clear plastic cup with sand and allowing her to burrow. A day after she burrowed, a male was introduced and the interactions on the surface of the sand were videorecorded through the clear plastic cup. In some instances only the first half-hour of copulation was video-recorded. In these instances the copulating pair was watched to note the duration of copulation. The end of copulation was taken at the moment when the spiders physically separated.

Vouchers of all species studied are deposited at the Mississippi Entomological Museum at Mississippi State University, Mississippi State, Mississippi. Table 1 summarizes the species and collecting localities for all individuals used in this study. Observations by Dondale and Redner were field observations made shortly after the spiders were collected. Localities for these species are provided in Table 2. Additional observations were provided by T. Kronestedt and J. Rovner. The cladograms were produced using the computer program MacClade (Maddison & Maddison 1992).

RESULTS

Copulatory pattern, intraspecific variation.—The overall pattern of palpal insertion and hematodochal expansion showed little intra-specific variation in the species where we were able to observe multiple individuals (*S. crassipes*, *S. duplex*, *S. ocreata*, *S.* nr *ocreata*, *S. retrorsa* and *G. rogersi*; Tables 1, 2), suggesting that there is not much variability in the overall pattern within a species when the first hour of copuation is observed. However, we also observed a few instances in which a male mounted a female facing the wrong direction or was unable to engage the palp in the epigynum apparently because his position was wrong. *Hogna helluo* (Walckenaer 1837) showed some variability in insertion pattern (Nappi 1975; Dondale & Redner unpubl.; Table 2), and one observation of the insertion pattern of *Rabidosa rabida* was inconsistent with other studies (Kaston 1936; compare with Montgomery 1903; Table 2). These observations suggest that conclusions of patterns based on single observations warrant some caution.

Copulatory pattern, interspecific variation.—Copulatory patterns varied both in the number of insertions on a side as well as the number of expansions of the hematodocha per insertion when different species were compared (Table 2; Figs. 1, 2). In four of the six *Pardosa* species observed by Dondale & Redner, members of the subfamily Pardosinae showed a single insertion on a side but with multiple expansions of the hematodocha with each insertion (Dondale & Redner unpubl. data; Table 2). In the subfamilies Sosippinae, Venoniinae and Allocosinae, all examples so far (four species total) demonstrate single insertions of the palps and multiple expansions of the hematodocha.

In the "*Lycosa* group" of the subfamily Lycosinae (as defined by Dondale 1986), *Arctosa littoralis* and *A. sanctaerosae* both showed a single insertion with a single expansion of the hematodocha. Both of these species are burrowing spiders, although only the latter is an obligate burrower. *Alopecosa* spp. and *Hygrolycosa* sp. both demonstrated single insertions of the palps with many expansions of the hematodocha (Kronestedt 1979 and pers. comm.).

In the "*Trochosa* group" of the Lycosinae there is remarkable consistency in *Schizocosa* species: 12 species examined to date demonstrated the pattern of multiple insertions on a side with a single expansion per insertion (Table 2; Figs. 1, 2). The 12 species of *Schizocosa* are from four different species groups within the genus (Stratton unpubl. data). This pattern held

Table 1.—Summary of taxa observed in this study. Collection locality (state and county) and dates are provided as are number of trials, courtships and copulations observed. (MS = Mississippi, AL = Alabama, FL = Florida, LA = Louisiana, OH = Ohio, TX = Texas, KY = Kentucky).

Species name	Locality	Date collected	Date of observations	# of trials/ # copulations
Arctosa littoralis (Hentz 1844)	MS. Grenada Co.	21 May 1994	9 June 1994	2/1
Arctosa sanctaerosae Gertsch & Wallace 1935	AL. Baldwin Co.	13 May 1994	19 May 1994	1/1
Geolycosa rogersi Wallace 1942	MS. Lafayette Co.	17, 23 March 1996	19 April 1996	3/3
Gladicosa bellamyi (Gertsch & Wallace 1937)	MS. Washington Co.	9 April 1993	29 April 1993	2/1
Hogna georgicola (Walckenaer 1837)	FL. Alachua Co.	4 May 1993	28 June 1993	1/1
Isohogna sp. A	AL. Baldwin Co.	13 May 1994	19 May 1994	4/1
Isohogna lenta (Hentz 1844)	MS. Marshall Co.	2 June 1994	14 June 1994	2/1
Rabidosa hentzi (Banks 1904)	AL. Baldwin Co.	14 May 1994	19 May 1994	8/2
Rabidosa punctulata (Hentz 1944)	MS. Tate Co.	25 Oct. 1995	20 Nov. 1995	2/1
Rabidosa rabida (Walckenaer 1837)	LA. Cameron Parish	22 May 1993	2 July 1993	2/1
Schizocosa avida (Walckenaer 1837)	MS. Marshall Co.	1 June 1993	26, 28 June 1993	5/2
S. crassipes (Walckenaer 1837)	FL. Alachua Co.	4 May 1993	4 June 1993	12/1
Schizocosa sp. nr. *crassipes*	MS. Grenada Co.	13 April 1995	18–31 May 1995	10/5
	TX. Nacogdoches Co.	12 April 1995	5 June 1995	2/2
S. duplex Chamberlin 1925	FL. Santa Rosa Co.	21 March 1995	April 1995	10/4
S. floridana Bryant 1934	FL. Alachua Co.	3 May 1993	9 May 1993	1/1
S. ocreata (Hentz 1844)	FL. Alachua Co.	3 May 1993	9 May 1993	
	OH. Clermont Co.	Fall 1994	Dec. 1994	53/26
Schizocosa sp. nr. *ocreata*	MS. Washington Co.			
	Stoneville Woods	14 April 1995	19–31 May 1995	10/8
	Leroy Percy St. Pk.	13 April 1995	19–31 May 1995	10/8
S. retrorsa (Banks 1911)	MS. Marshall Co.	29 June 1993	8 July 1993	5/1
	MS. Lafayette Co.	28 April 1993	30 June 1993	5/1
S. stridulans Stratton 1991	KY. Powell Co.	16–23 June 1993	29 June 1993	2/1
S. saltatrix (Hentz 1844)	MS. Lafayette Co.	10 March 1993	20–21 April 1993	22/1
Schizocosa sp. nr. *saltatrix*	MS. Adams Co.	9 April 1993	16–23 April 1994	4/2
Schizocosa n. sp.	MS. Lafayette Co.	15 June 1993	13 July 1993	5/2
	LA. Natchitoches Par.	23 May 1993	10 July 1993	5/3
Trochosa avara Keyserling 1877	MS. Tate Co.	25 Oct. 1995	Nov. 1, 1995	3/1

true for all instances where numerous populations were observed (Table 2). This pattern is consistent with four species of *Trochosa* studied by Engelhart (1964) in Europe. However, in *Trochosa avara* Keyserling 1877 (single observation from southeastern USA), we observed multiple insertions of each palp and multiple expansions of the hematodocha without disengaging. The failure to disengage the palp before each expansion made this individual different from the *Schizocosa* species and other *Trochosa* species. More observations on *Trochosa avara* and on the other North American *Trochosa* species are needed.

There was more variability in *Hogna* species than the *Schizocosa* species (Dondale & Redner unpubl. data; Table 2; Figs. 1, 2). *Hogna helluo*, *H. aspersa* (Hentz 1844), and *H. frondicola* (Emerton 1885) each showed a single insertion on a side (expansions of hematodocha not recorded); *H. radiata* showed multiple insertions with one expansion per insertion, as did *H. georgicola* and one example of *H. helluo*.

There was also variablility in the *Geolycosa* species although the number of observations are still relatively few for this genus. *Geolycosa rogersi* showed a single insertion on a side with a single expansion of the hematodocha (Table 2). *Geolycosa domifex* (Hancock 1899) performed multiple insertions on each side. The number of hematodochal expansions was not observed (Dondale & Redner unpubl. data).

The *Rabidosa* spp. and *Gladicosa gulosa* (Walckenaer 1837) showed a single insertion on a side and a single expansion of the hematodocha. *Gladicosa bellamyi* showed multiple insertions on a side with a single expansion per insertion. *Isohogna lenta* (a single individual) switched between a single insertion with one expansion, and multiple insertions with multiple expansions, making it the most variable individual observed in this study. A second species of *Isohogna* (species A) showed multiple insertions with multiple expansions.

Duration of copulations.—Within the "*Trochosa* group" copulations ranged in duration from 5 min for *Geolycosa domifex* and *G. rogersi* to over 8 h for *S. saltatrix*. The *Schizocosa* spp. ranged from 1–8 h with most values from 1–4 h (Table 2); *Trochosa* spp. ranged from 20 min–6 h 48 min. The copulations for *Hogna* species were all longer than 1 h except for a single observation reported by Kaston (1936).

Within the "*Lycosa* group" the *Arctosa* spp. both showed very short copulations (18–33 sec). There was variability in the durations of copulation reported on and observed in *Gladicosa* spp. (short times reported by Kaston for *G. gulosa*; a longer time was observed for *G. bellamyi*). Copulation duration for *Rabidosa* spp. ranged from 25 min–1 h 30 min.

DISCUSSION

Comparisons between subfamilies of Lycosidae.—Costa & Sotelo (1994) reported that there appears to be some consistency in the copulatory pattern within the lycosid subfamilies identified by Dondale (1986). For example, in the Sosippinae, Venoniinae, and Allocosinae, the three most basal subfamilies, all known examples showed a single insertion on a side with multiple expansions of the hematodocha (see Figs. 1, 2). These examples included *Porrimosa lagotis* (Holmberg 1876), subfamily Sosippinae (Costa 1982 *in* Costa & Sotelo 1994); *Pirata* Sundevall 1833 sp., subfamily Venoniinae (Gerhardt 1924 *in* Costa & Sotelo 1994); and *Allocosa* Banks 1900 sp. subfamily Allocosinae (Costa unpubl. data).

Costa & Sotelo (1994; see also Kaston 1936) summarized five examples of copulatory pattern in the Pardosinae. These examples all showed a single insertion on a side but the authors did not report the number of expansions. Dondale & Redner (unpubl. data) added six more species in *Pardosa*; with two exceptions these showed single insertions with multiple expansions (Figs. 1, 2). This suggests that no one pattern characterizes this genus and subfamily and that there is more variability than noted by Costa & Sotelo (1994).

The Lycosinae, the most derived subfamily according to Dondale's 1986 study, stands out in having all combinations of insertions and expansions (Figs. 1, 2). The vast majority of the studies of insertion pattern have been in Lycosinae. It appears that when numerous studies are available at the subfamily level, there is variability in copulatory pattern. Clearly, more studies are needed in the other subfamilies of lycosids to more fully understand the evolution of patterns of copulation.

Comparisons within the Lycosinae.—Dondale (1986) suggested that the Lycosinae can be subdivided into two groups based on palpal characteristics: the "*Lycosa* group" (including *Lycosa* Latreille 1804 [Europe only], *Arctosa*, *Alopecosa*, *Varacosa* Chamberlin & Ivie 1942 and *Hygrolycosa*); and the "*Trochosa* group" (including *Trochosa*, *Hogna*, *Geolycosa*, *Schizocosa*, *Gladicosa*, and *Rabidosa*). Within species of the "*Lycosa* group" (six species examined in this study) all individuals demonstrated single insertions on a side, but there was variability in the number of expansions (Table 2). Within species of the "*Trochosa* group" (33 species examined in this study), there was the consistent pattern noted for species of *Schizocosa* and most of

Table 2.—Pattern of palpal insertion and duration of copulation for many Lycosoidea, including Ctenidae, Pisauridae and Lycosidae plus examples from the Amaurobiidae and the Agelenidae. This table includes examples from the literature, unpublished observations by C. Dondale, J. Redner, J. Rovner and T. Kronestedt, in addition to the species observed by us. Initials for state localities as in Table 1. Sample sizes for durations are $n = 1$ unless otherwise noted by multiple entries or by means. Notes in table are as follows. [1] The pattern of expansions of hematodocha not stated for *Ancylometes* and *Thalassius.* [2] *Pardosa dromaea* showed multiple "pulses while the hematodocha remained expanded" (Dondale & Redner unpubl. data). [3] For *Alopecosa* and *Hygrolycosa,* for each palpal application, numerous hematodochal swellings occurred. There was no disengagement of the palp between the numerous swellings, (Kronestedt, pers. comm.). [4] Expansions not observed for some observations of *Hogna helluo,* nor for observations of *Hogna aspersa, Hogna frondicola, Hogna radiata, Schizocosa avida* (Ontario), *Schizocosa communis* and *Geoloycosa domifex,* (Dondale & Redner, unpublished data). [5] In *Rabidosa rabida,* "contrary to Montgomery's observation, there was not always strict alternation in the use of the palps" (Kaston 1936). [6] For *Hololena adnexa* "each palpus was used in a single long series of insertions" (Fraser 1986), number of expansions per insertion not specified.

	Number of insertions on a side before switching sides		Number of expansions of hematodocha per insertion		
Species, location of study, source	one	more than one	one	more than one	Duration
Family Ctenidae					
Cupiennius salei	XX			XX	25 min
Melchers 1963					
Family Pisauridae					
Pisaurina mira	XX		XX		
Bruce & Carico 1988					
Ancyclometes bogotensis[1]	XX				10–15 min
Merrett 1988					
Thalassius spinosissimus[1]	XX				
Sierwald 1988					
Dolomedes tenebrosus	XX				4–5 min
Sierwald and Coddington 1988					
Dolomedes scriptus ($n = 4$)	XX				
CT. New Haven Co.					5, 15, 20, 30 sec
Kaston 1936					
Dolomedes fimbriatis ($n = 3$)	XX			XX	
Gerhardt 1926					
Pisaura mirabilis ($n = 3$)	XX			XX	
Gerhardt 1923					
Family Lycosidae, Subfamily Sosippinae					
Sosippus janus	XX			XX	
Rovner unpubl. data					
Porrimosa lagotis	XX			XX	
Costa 1982 *in* Costa & Sotelo 1994					
Family Lycosidae, Subfamily Venoniinae					
Pirata spp.	XX			XX	
Gerhardt 1924 *in* Costa & Sotelo 1994					
Family Lycosidae, Subfamily Allocosinae					
Allocoa sp.	XX			XX	
Costa unpubl.					

Table 2.—Continued.

Species, location of study, source	Number of insertions on a side before switching sides: one	more than one	Number of expansions of hematodocha per insertion: one	more than one	Duration
Family Lycosidae, Subfamily Pardosinae					
Pardosa concinna	XX			XX	15 min
Colorado					
Dondale & Redner unpubl. 1983					
Pardosa fuscula	XX			XX	15 min
Ontario					
Dondale & Redner unpubl. 1983					
Pardosa mackenziana	XX			XX	60 min
Ontario					
Dondale & Redner unpubl.					
Pardosa groenlandica					
Quebec	XX			XX	42 min
Dondale & Redner unpubl. 1972					
Colorado (n = 3)	XX			XX	20, 68 & 15 min
Montana		XX		XX	45 min
Dondale & Redner unpubl. 1985					
Pardosa dromaea[2]					
Alberta	XX		XX		25–30 min
Dondale & Redner unpubl. 1985					
Pardosa amentata (n = 3)	XX		XX		
Gerhardt 1923					
Family Lycosidae, Subfamily Lycosinae, "Lycosa group"					
Alopecosa pulverulenta[3]	XX			XX	
Sweden					
Kronestedt 1979					
Alopecosa aculeata	XX			XX	
Sweden					
Kronestedt 1979					
Alopecosa taeniata	XX			XX	
Sweden					
Kronestedt 1979					
Arctosa littoralis					
MS. Grenada Co.	XX		XX		18 sec
this study					
Arctosa sanctaerosae					
AL. Baldwin Co.	XX		XX		46, 33 sec
this study					
Hygrolycosa rubrofasciata[3]	XX			XX	
Sweden					
Kronestedt 1979					
Subfamily Lycosinae, "*Trochosa* group"					
Geolycosa domifex[4]		XX			5 min
Canda, Ontario					
Dondale & Redner 1990					
Geolycosa rogersi (n = 3)	XX		XX		$\bar{x}$ = 7 min 9 sec
this study					

Table 2.—Continued.

Species, location of study, source	Number of insertions on a side before switching sides: one	more than one	Number of expansions of hematodocha per insertion: one	more than one	Duration
Gladicosa bellamyi					
MS. Washington Co.		XX	XX		1 hr 15 min
this study					
Gladicosa gulosa					
CT. New Haven Co.	XX		XX		10 min, 30 min
Kaston 1936					
Hogna georgicola		XX	XX		58 min
FL. Alachua Co.					
this study					
Hogna helluo					
CT. New Haven Co.	XX		XX		8 min
Kaston 1936					
CT. Central Ct. State Coll.			XX		
Nappi 1965	XX				
Dondale & Redner unpubl.[4]		XX			1 h +
Hogna aspersa	XX				1 h 45 min
Dondale & Redner unpubl.[4]					
Hogna frondicola	XX				2 h 45 min
Dondale & Redner unpubl.[4]					
Hogna radiata (Europe)		XX	XX		1 h 3 min
Dondale & Redner unpubl.[4]					
Isohogna sp. A					
AL. Baldwin Co.		XX		XX	30 min
this study					
Isohogna lenta					
MS. Marshall Co.	XX		XX		
this study					
Rabidosa hentzi					
AL. Baldwin Co.	XX		XX		25 min, 40 min
this study					
Rabidosa punctulata					
OH. Athens Co.					
Rovner unpubl. data	XX		XX		
MS. Tate Co.					
this study	XX		XX		
Rabidosa rabida					
MS. Lafayette Co.	XX		XX		1 h 30 min
this study					
OH, Athens Co.	XX		XX		1 h
Rovner 1972					
CT, New Haven Co.[5]	XX	XX	XX		71 min
Kaston 1936; Montgomery 1903					
Schizocosa avida					
MS. Marshall Co.		XX	XX		2 h 15 min
this study					
OH. Athens Co.		XX	XX		
Rovner 1973					
Ontario		XX			2 h 55 min
Dondale & Redner unpubl.					

Table 2.—Continued.

Species, location of study, source	Number of insertions on a side before switching sides: one	Number of insertions on a side before switching sides: more than one	Number of expansions of hematodocha per insertion: one	Number of expansions of hematodocha per insertion: more than one	Duration
Schizocosa bilineata		XX	XX		
Montgomery 1903					
Schizocosa communis					
Ontario		XX			1 h 3 min
Dondale & Redner unpubl. 1966[5]					
Schizocosa crassipes					
FL. Alachua Co.		XX	XX		
this study					
Schizocosa sp. nr. *crassipes*					
MS. Grenada Co.		XX	XX		$\bar{x}$ = 2h 24 min
this study (n = 5)					
MS. Claiborne Co.		XX	XX		4 h 35 min
this study					
TX. Nacogdoches Co.		XX	XX		
this study (n = 2)					
Schizocosa duplex					
FL. Santa Rosa Co.		XX	XX		$\bar{x}$ = 1 h 31 min
this study (n = 4)					
Schizocosa floridana					
FL. Alachua Co.		XX	XX		3 h 31 min
this study (n = 2)					
Schizocosa ocreata					
FL. Alachua Co.		XX	XX		3 h 30 min,
this study					2 h 28 min
OH. Hocking Co.		XX	XX		1–4 h
Stratton & Uetz 1983					
OH. Brown Co.		XX	XX		1–4 h
Stratton & Uetz 1983					
OH. Clermont Co.		XX	XX		$\bar{x}$ = 3 h 28 min
this study (n = 26)					
Schizocosa sp. nr. *ocreata*					
MS. Washington Co.		XX	XX		$\bar{x}$ = 2 h 17 min
this study (Stoneville, Leroy Percy) (n = 15)					
MS. Adams Co.		XX	XX		1 h 40 min
this study					
Schizocosa retrorsa					
MS. Marshall Co.		XX	XX		2 h 30 min
this study					
MS. Lafayette Co.		XX	XX		2 h 40 min
this study					
Schizocosa rovneri					
KY. Boone Co.		XX	XX		1–4 h
Stratton & Uetz 1983					
Schizocosa saltatrix					
MS. Lafayette Co.		XX	XX		>8 h
this study					
OH. Athens Co.		XX	XX		$\bar{x}$ = 2 h 48 min
Rovner 1973, 1974					

Table 2.—Continued.

Species, location of study, source	Number of insertions on a side before switching sides: one	more than one	Number of expansions of hematodocha per insertion: one	more than one	Duration
Schizocosa sp. nr. *saltatrix*					
MS. Adams Co.		XX	XX		
this study (n = 2)					
Schizocosa stridulans					
MS. Lafayette Co.		XX	XX		
this study					
IL. Mason Co.		XX	XX		
Stratton unpubl.					
Schizocosa n. sp.					
MS. Lafayette Co.		XX	XX		1 h 55 min, 1 h 55 min
this study (n = 2)					
LA. Natchitoches Parish		XX	XX		1 h 30 min, 2 hr 10 min
this study (n = 2)					
Trochosa avara		XX		XX	
MS. Tate Co.					
this study					
Trochosa terricola		XX	XX		$\bar{x}$ = 2 h 9 min
Engelhardt 1964					
Trochosa ruricola		XX	XX		$\bar{x}$ = 20 min
Engelhardt 1964					
Trochosa spinipalpis		XX	XX		$\bar{x}$ = 1 h 32 min
Engelhardt 1964					
Trochosa robusta		XX	XX		$\bar{x}$ = 2 h 24 min
Engelhardt 1964					(max 6 h 48 min)
Family Amaurobiidae					
Ixeuticus martius		XX	XX		2 h 24 min
Costa 1993					
Amaurobius ferox (n = 2)	XX		XX		
Gerhardt 1923					
Amaurobius fenestralis	XX		XX		
Gerhardt 1924a					
Titanoeca quadriguttata (n = 2)	XX		XX		
Gerhardt 1928					
Family Agelenidae					
Hololena adnexa[6]		XX	XX		
Fraser 1986					
Histopona torpida	XX			XX	
Gerhardt 1927					
Coelotes atropos (n = 2)	XX		XX		
Gerhardt 1928					

the *Trochosa* but variability in the copulation pattern in *Hogna*, *Isohogna*, and *Geolycosa* (Table 2; Figs. 1, 2). With the exception of a single individual observed by Kaston (1936), the *Rabidosa* were consistent with alternating insertions and a single expansion.

Comparisons with other Lycosoidea.—The sister group to the Lycosidae is currently

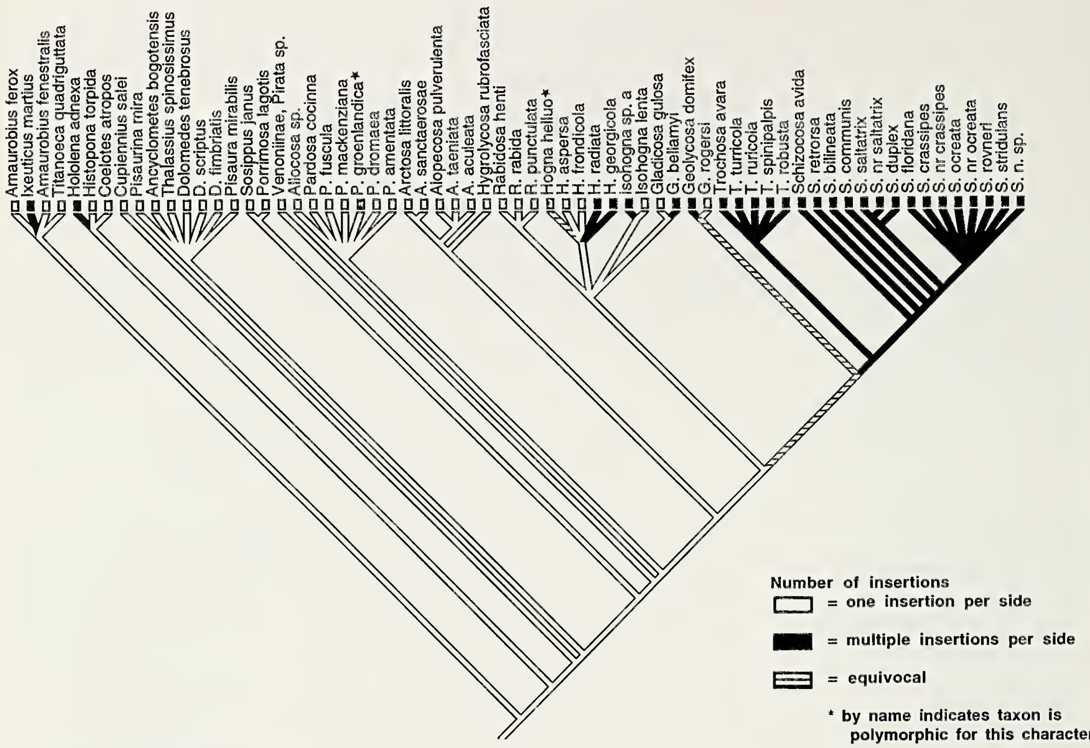

Figure 1.—Phylogeny of Lycosoidea (based on Griswold 1993; Carico 1993; Sierwald 1990), subfamilies of Lycosidae (based on Dondale 1986) plus Agelenidae and Amaurobiidae (from Coddington & Levi 1991) with overlay of pattern of insertion. The arrangement of *Schizocosa* species is based on an unpublished study; the *Rabidosa*, *Hogna* and *Isohogna* are each shown as polytomies that are clustered by genus name. Open bar is one insertion per side; filled bar is multiple insertions per side. Multiple insertions evolved either on the branch that includes *Geolycosa*, *Trochosa* and *Schizocosa* or on the branch that includes *Trochosa* and *Schizocosa*. The large lycosids of the "*Trochosa* group" (*Rabidosa*, *Hogna*, *Isohogna*, *Gladicosa* and *Geolycosa*) are variable for this character. The "*Lycosa* group" of the Lycosinae (*Arctosa*, *Alopecosa*, and *Hygrolycosa*) all show one insertion per side. Two species are polymorphic for this character; these are indicated with an asterisk.

recognized as the Trechaleidae (Carico 1986, 1993; Sierwald 1990; Griswold 1993); the Pisauridae and Ctenidae are also closely related (Figs. 1, 2) (Coddington & Levi 1991).

The insertion pattern for the Trechaleidae is not known (Carico pers. comm.). Members of four genera of the Pisauridae showed the pattern of alternating insertions (Table 2; Fig. 1). In *Pisaurina mira* (Walckenaer 1837) there was "a total of 3–5 insertions with a shift in the body between each insertion" (Bruce & Carico 1988); the palpal bulb expanded for 20–30 sec. Likewise, in *Ancylometes bogotensis* "each palp was inserted several times, alternately; the mating lasting about 10–15 min" (Merrett 1988). In her study of the African species of *Thalassius spinosissimus* Karsch 1876, Sierwald (1988) noted that both palpi were used alternately, with 3–5 insertions occurring during copulation. Insertions lasted 5–20 sec for each palp. In these studies, the number of expansions was not noted.

The insertion pattern for *Cupiennius salei* Keyserling 1877, the one available example of Ctenidae, was of multiple expansions of the hematodocha during a single insertion followed by a switch to the opposite side. The ctenid showed 96 expansions in 12 min and typically only two insertions (one on each side) (Melchers 1963).

For the examples available in the Ctenidae and the Pisauridae, there was a single insertion on a side. The basal subfamilies of the Lycosidae also showed a single insertion on a side. This suggests that for insertion pattern, a single insertion on a side before switching

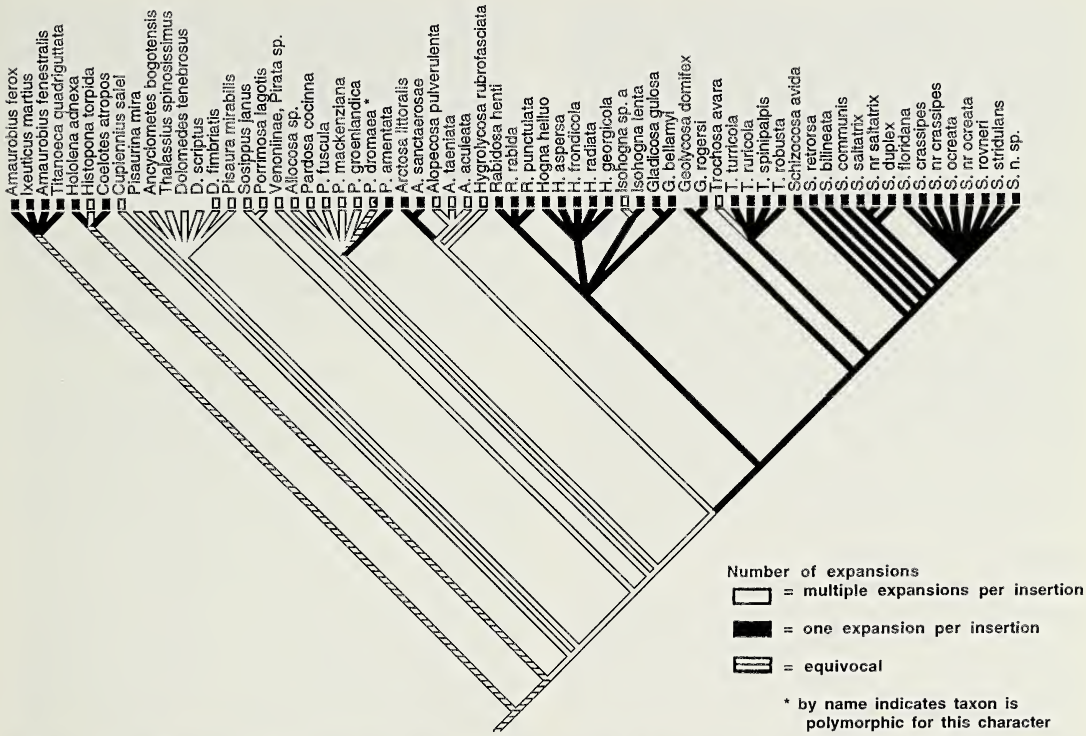

Figure 2.—Phylogeny of Lycosoidea plus Agelenidae and Amaurobiidae with overlay of pattern of embolus expansion. Arrangement of taxa is as in Figure 1. Open bar is multiple expansions per insertion; filled bar is one expansion per insertion. A single expansion per insertion in seen in most of the "*Trochosa* group" of the Lycosinae. The "*Lycosa* group" (*Arctosa*, *Alopecosa* and *Hygrolycosa*) are mixed for this character. One species is polymorphic for this character and is indicated with an asterisk.

may be the primitive pattern and multiple insertions on a side is the derived pattern (Fig. 1).

There are too few examples from the Ctenidae and Pisauridae to draw strong conclusions about the origin of the pattern of expansions (for several of the examples, the pattern of expansion was not given) (Fig. 2). However, the presence of multiple expansions of the hematodocha in *Cupiennius salei*, and in the three basal subfamilies of the Lycosidae suggests that multiple expansions may be primitive. An increase in the number of observations in the other subfamilies of lycosids will help clarify this picture.

The large number of different patterns seen in the Lycosinae may partly be a function of the number of studies done on this group; and since the sample sizes for the other subfamilies of lycosids and families of Lycosoidea are small, these data should be considered preliminary. Also, the diversity of patterns seen in the Lycosinae, and especially the "*Trochosa* group", suggests that the copulatory pattern may be fairly maleable in evolution, at least within that clade.

Evolution of copulatory pattern in Lycosidae.—It appears that in some taxa (such as *Schizocosa* spp.) the pattern of copulatory behavior shows some consistency while in other taxa (such as *Hogna* spp.) the overall pattern may vary between closely related species. It is interesting to speculate on the possible function of the differences in insertion and expansion patterns. The pattern seen consistently in *Schizocosa*, that of multiple insertions on one side, with one expansion of the hematodocha per insertion and palpal grooming between insertions, might allow for multiple opportunities for copulatory courtship (Eberhard 1994). Prior to each insertion in *Schizocosa* spp., the male scrapes the sides of the female's abdomen, and while there may not be many sensory sensilla directly on the female's epigynum (Huber 1993), there are many sensilla on the female's abdomen in the

region surrounding the epigynum. Additionally, in the *S. ocreata* species group, males have a finger-like process on the palea of the palpal bulb and each expansion of the hematodocha results in the paleal process scraping or pinching the sides of the epigynum (unpubl. data based on high magnification video from the ventral aspect of *Schizocosa* sp. nr. *ocreata*). This is consistent with Eberhard's sexual selection prediction (Eberhard 1985, 1986) that species-specific traits found on male genitalia are likely to be in direct contact with the female. Each separate insertion could therefore provide for stimulation of the female both as the palp of the male scrapes the side of her abdomen and then additionally (for the *S. ocreata* group) from the paleal process as it pinches the sides of the epigynum as the hematodocha expands.

The species that showed multiple insertions on a side with a single expansion during each insertion had far longer copulations than the species that had multiple expansions (Table 2). Why should copulations be so long in these spiders? A long copulation may be a means for a male to restrict access to that female by other males (seen in *S. avida* [Walckenaer 1837], J. Latimore pers. comm.). A second possibility is that within the *Schizocosa* and *Trochosa* there is "in-copula" courtship (Eberhard 1994) as discussed above. A long copulation with many courtship movements on the part of the male could allow for many opportunities for the female to assess the male and for the male to induce favorable female responses. A third possibility is that the morphology of the male and female genitalia does not constitute as good a "fit" as a lock and key description may imply. Multiple insertions may be a mechanism that would assure at least one or a few successful insertions of the embolus by the male into the female. On several occasions we have observed males that mounted the female backwards and attempted to copulate from the wrong position. In other cases, the male oriented correctly but was not quite in the right position for the palp to engage with the epigynum. Multiple insertions would increase the probability of getting some insertions right.

The obligate burrowing spiders, *Arctosa sanctaerosae* and *Geolycosa* species all showed short copulations with the copulations happening at the top of the burrow. We observed three instances in which males of *G. rogersi* attempted to copulate while a female was not in a burrow; in each of these, the male mounted backwards and did not copulate successfully. In the burrowing species, the burrow may be critical for correct orientation of the copulating pair.

Further work on copulation duration and pattern and in particular, studies on the timing of sperm transfer are necessary to further clarify the evolution of this behavior in lycosids.

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CLADISTIC ANALYSIS OF THE *ATYPOIDES* PLUS *ANTRODIAETUS* LINEAGE OF MYGALOMORPH SPIDERS (ARANEAE, ANTRODIAETIDAE)

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ABSTRACT. Cladistic analyses of the antrodiaetid spider genera *Atypoides* O.P.-Cambridge 1883 and *Antrodiaetus* Ausserer 1871 yield a much more completely resolved phylogeny than that proposed by Coyle in 1971. Twenty-nine potentially informative characters were used in the analyses, which were performed using PAUP's *a posteriori* weighting options. Three independent analyses were performed, each with a different outgroup. These outgroups were 1) the antrodiaetid genus *Aliatypus* Smith 1908, the putative sister group of *Atypoides* plus *Antrodiaetus*, 2) *Aliatypus gulosus* Coyle 1974, the most primitive *Aliatypus* species, and 3) a hypothetical ancestral taxon based on character states found in *Aliatypus* and the Atypidae, the latter being the putative sister group of the antrodiaetids. These three analyses produced a total of eight most parsimonious trees which support the following principal conclusions: 1) *Atypoides*, as defined by Coyle, is paraphyletic (*Atypoides riversi* O. P.-Cambridge 1883 plus *At. gertschi* Coyle 1968 share with *Antrodiaetus* a common ancestor not shared with *At. hadros* Coyle 1968). 2) *Antrodiaetus roretzi* (L. Koch 1878) is a relict species which shares a unique common ancestor with all other *Antrodiaetus* species. 3) Coyle's *unicolor* group of nine *Antrodiaetus* species is paraphyletic; six of these form a recently-derived clade, (*Antrodiaetus occultus* Coyle 1971 (*An. yesoensis* [Uyemura 1942], *An. cerberus* Coyle 1971, (*An. montanus* [Chamberlin & Ivie 1933], (*An. pugnax* [Chamberlin 1917], *An. hageni* [Chamberlin 1917]), and the other three species, *An. pacificus* (Simon 1884), *An. robustus* (Simon 1890), and *An. unicolor* (Hentz 1841), are derived from more ancestral stock. 4) Coyle's *lincolnianus* group of three *Antrodiaetus* species, *An. lincolnianus* (Worley 1928), *An. stygius* Coyle 1971, and *An. apachecus* Coyle 1971, represents a valid clade. Our phylogeny suggests that two separate vicariance events led to the evolution of the two east Asian members of this otherwise North American assemblage. Vicariance events that are indicated by geological evidence and consistent with our phylogeny are postulated to account for the present distribution of North American species. New putative synapomorphies of *Antrodiaetus*, and of *Antrodiaetus* plus *Atypoides*, are proposed.

The monophyly of the Antrodiaetidae (defined to include *Aliatypus, Antrodiaetus* and *Atypoides*) has survived the collapse of the Atypoidea brought about by the recent cladistic revolution in arachnology (Platnick & Gertsch 1976; Platnick 1977). Although all phylogenies of the Mygalomorphae published within the last decade postulate that these three genera form a monophyletic Antrodiaetidae (Raven 1985; Eskov & Zonshtein 1990; Coddington & Levi 1991; Goloboff 1993), Coyle (1994) has drawn attention to the tenuousness of this hypothesis, arguing that many of the proposed synapomorphies may be either plesiomorphies or homoplasies.

The three species of *Atypoides* and 13 species of *Antrodiaetus* were hypothesized by Coyle (1968, 1971) to form a monophyletic group. This relationship has been supported by the following putative synapomorphies: 1) a strongly developed inner conductor sclerite (ICS) that surrounds the embolus and has a tip which is clearly separate from the outer conductor sclerite (OCS) (Raven 1985; Coyle 1994); 2) reduction of the anterior lateral spinnerets (ALS) (Coyle 1971; Raven 1985); 3) the presence of a cheliceral apophysis (or its vestige) in mature males (Coyle 1971; Raven 1985); 4) a longitudinal thoracic fovea (Coyle 1971, 1994). Coyle (1994) has discussed the problematic nature of synapomorphy 2, ex-

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Table 1.—Quantitative character values for *Atypoides* and *Antrodiaetus* species. Range, mean, and standard deviation (if $n > 4$) are given for all ratio characters; range and mean only for meristic characters. PTT/PTL and ITL/IML are male characters; all others are female characters. See Methods section for character definitions.

	n females	*n* males	CMT	IMS	IVCTR
At. hadros	6	15	2–5 2.9	8–10 8.7	3–4 3.5
At. riversi	86	25	6–33 18.3	17–32 23.0	6–11 7.3
At. gertschi	57	20	9–26 17.7	18–35 23.6	4–10 7.2
An. roretzi	2	2	6	15	4
An. pacificus	56	105	9–24 16.8	9–15 12.3	1–6 4.0
An. robustus	13	11	11–18 13.9	9–14 10.6	2–5 3.6
An. unicolor	225	104	6–23 12.0	9–15 11.6	1–6 3.5
An. occultus	0	21			
An. yesoensis	1	2	7	10	4
An. cerberus	4	4	12–19 15.7	11–13 11.7	4–5 4.5
An. montanus	12	23	16–29 21.9	12–16 12.9	3–5 3.9
An. hageni	7	8	13–18 15.1	13–15 13.7	2–5 4.0
An. pugnax	24	24	8–17 12.1	9–13 11.1	4–6 4.2
An. lincolnianus	2	6	23–27	13	0–1 0.5
An. stygius	3	8	14–19 17.0	11–13 12.0	0–2 1.3
An. apachecus	3	8	10–16 13.0	11–12 11.3	0–2 1.0

plaining that the ALS of *Atypoides* may be at least as well developed as those of the atypids, but the other three synapomorphies appear to be valid. We have identified a new putative synapomorphy of *Atypoides* plus *Antrodiaetus*: these taxa share a spermathecal bowl—apparently either the result of the sclerotization of the proximal portion of the spermathecal bulb itself or of the expansion of the distal end of the sclerotized spermathecal stalk (Coyle 1968, figs. 80–94; 1971, figs. 270–311)—which is not found in *Aliatypus* or the Atypidae, and may be unique among the Mygalomorphae.

Coyle (1971) constructed a working hypothesis of the phylogeny of the *Atypoides* plus *Antrodiaetus* lineage using a protocladistic approach. However, much of that tree was unresolved. Eight of the ten characters used to construct that phylogeny have been used in our current study, although some of these have been redefined, quantified, or split into several discrete characters. By modifying these characters, utilizing 14 ad-

Table 1.—Extended.

IML/CL	ITL/IML	PTT/PTL	IVML/CL
0.36–0.38 0.38 ± 0.01	0.81–0.86 0.84 ± 0.01	0.42–0.47 0.45 ± 0.01	0.50–0.53 0.52 ± 0.01
0.51–0.65 0.56 ± 0.03	0.66–0.77 0.71 ± 0.03	0.32–0.50 0.46 ± 0.03	0.55–0.70 0.63 ± 0.03
0.50–0.59 0.55 ± 0.02	0.71–0.80 0.75 ± 0.02	0.30–0.33 0.32 ± 0.01	0.70–0.86 0.77 ± 0.04
0.45–0.46	0.75–0.76	2.78	0.57–0.58
0.42–0.51 0.47 ± 0.02	0.65–0.81 0.72 ± 0.04	0.33–0.48 0.40 ± 0.03	0.51–0.65 0.58 ± 0.03
0.38–0.42 0.40 ± 0.01	0.77–0.83 0.80 ± 0.02	0.40–0.47 0.43 ± 0.02	0.52–0.57 0.55 ± 0.02
0.35–0.48 0.44 ± 0.02	0.74–0.85 0.81 ± 0.03	0.38–0.54 0.45 ± 0.04	0.49–0.68 0.60 ± 0.04
	0.81–0.90 0.85 ± 0.02	0.45–0.49 0.47 ± 0.02	
0.41	0.95–0.99	0.45–0.47	0.56
0.43–0.46 0.44	0.92–0.93 0.93	0.39–0.41 0.40	0.62–0.67 0.65
0.44–0.52 0.48 ± 0.02	0.83–0.91 0.88 ± 0.02	0.35–0.40 0.38 ± 0.01	0.60–0.65 0.64 ± 0.02
0.43–0.48 0.46 ± 0.02	0.88–0.90 0.90 ± 0.01	0.37–0.41 0.39	0.61–0.65 0.64 ± 0.02
0.39–0.48 0.43 ± 0.02	0.82–0.91 0.88 ± 0.03	0.37–0.44 0.42 ± 0.01	0.56–0.65 0.60 ± 0.03
0.41–0.42	1.00–1.04 1.02 ± 0.02	0.23–0.24 0.24 ± 0.0	0.56
0.35–0.38 0.37	0.87–0.94 0.90 ± 0.02	0.31–0.34 0.32 ± 0.01	0.48–0.53 0.51
0.40–0.44 0.42	0.89–0.99 0.94 ± 0.04	0.29–0.34 0.33 ± 0.02	0.50–0.54 0.52

ditional characters, and employing modern cladistic methods, we hope to generate a phylogeny which more closely approaches real history.

METHODS

Following the methods of Coyle (1994), we searched for phylogenetically informative characters by carefully screening the descriptions, illustrations and quantitative character tables in Coyle (1968, 1971) for character states which distinguish two or more species from the rest. A total of 29 potentially informative characters were selected by this process and eventually used in the analyses. Nineteen of these characters were adopted from species descriptions and illustrations, three from a table of male leg I macrosetation, and seven (three meristic characters and four ratios of measurements used to represent proportions and shapes) from quantitative character tables. The data set contains ten genitalic characters (six male and four female) and 19 characters of somatic morphology. All eight

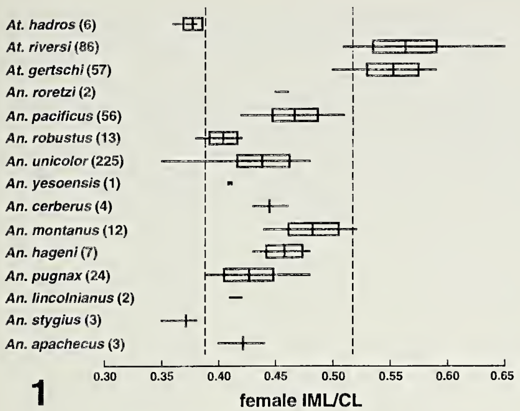
triple-state characters were treated as ordered because all appear to have discrete intermediate character states. The range, mean and standard deviation for each of the ratio and meristic characters are given in Table 1. These characters were selected from the much larger set of quantitative characters surveyed in this study because they distinguish clusters of species with nonoverlapping values or with mean values significantly different ($P < 0.05$) from other such clusters (see, for example, Figs. 1, 2). Thiele (1993) has argued convincingly and demonstrated with botanical data sets that quantitative (morphometric) characters are useful in cladistic analyses, and the second author has found this to be true in his cladistic analyses of other mygalomorph spider genera (Coyle 1994, 1995).

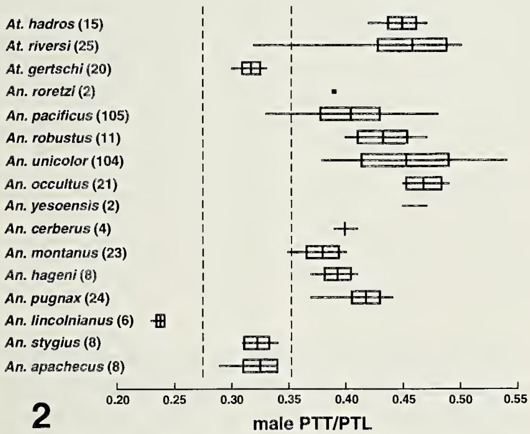
Three outgroup taxa were used to polarize character evolution: the genus *Aliatypus*, *Aliatypus gulosus*, and a hypothetical ancestral taxon. Despite problems with the putative synapomorphies that unite *Aliatypus* with the other antrodiaetids, current consensus places *Aliatypus* as the sister genus of the *Atypoides* plus *Antrodiaetus* lineage (Raven 1985; Goloboff 1993; Coyle 1994). *Aliatypus gulosus* is the most primitive *Aliatypus* species and shares with *Antrodiaetus* plus *Atypoides* certain apparently plesiomorphic traits of the male and female genitalia that have probably been modified in all other *Aliatypus* species (Coyle 1974, 1994). For both of these outgroups, character states were determined from data in Coyle (1974). The hypothetical ancestral taxon was based on the most probable primitive character states exhibited by species of *Aliatypus* and the family Atypidae, which is considered to be the sister group of the Antrodiaetidae (Raven 1985; Coddington & Levi 1991; Goloboff 1993) or, along with the mecicobothriids, part of the sister group of the antrodiaetids (Eskov & Zonshtein 1990). We determined these putative ancestral states by examining hypotheses and data on *Aliatypus* (Coyle 1974, 1994), *Sphodros* (Gertsch & Platnick 1980), and *Atypus* (Schwendinger 1989, 1990), and by studying specimens of *Sphodros rufipes* (Latrielle) and *Sphodros abboti* Walckenaer. The use of a hypothetical outgroup taxon was deemed desirable because *Aliatypus* appears to be a highly derived assemblage of species in which many ancestral conditions seem to have been modified, in part, at least, during an adaptive shift into a xerophyllic/trapdoor adaptive zone (Coyle & Icenogle 1994).

Independent cladistic analyses were performed using each of the three outgroup taxa. Each data matrix was analyzed using the branch and bound tree searching algorithm of PAUP version 3.1 for the Apple Macintosh (Swofford 1993). Successive *a posteriori* character weighting of the resulting trees was performed using each of the three options available in PAUP: the consistency index (CI), the retention index (RI), and the rescaled consistency index (RC). Further analysis was conducted using MacClade version 3.0 (Maddison & Maddison 1992).

Character states.—The character state data used in the analysis are presented in Table 2 and Fig. 3. Abbreviations and definitions for measurements, meristic characters and structures are given in Coyle (1968, 1971). In brief, they are: ALS, anterior lateral spinnerets; CL, carapace length; CMT, number of microteeth on each chelicera; ICS, inner conductor sclerite of the male palpus; IML, length of metatarsus I; IMS, number of ensiform macrosetae (spines) on female metatarsus I; ITL, length of tibia I; IVCTR, number of teeth on retrolateral claw of left tarsus IV; IVML, length of metatarsus IV; OCS, outer conductor sclerite of the male palpus; PTL, length of palpal tibia; PTT, maximum diameter of palpal tibia, in lateral view. An expanded treatment of each character used in the analysis follows. Characters 6, 10, 11, and 12 describe conditions that are visible when the prolateral surface of the left male palp is viewed with the conductor tips pointing upwards (as in Coyle 1971, figs. 188, 190, etc.).

1. Number of microteeth on female chelicera: 0 = large (mean CMT > 11); 1 = small (mean CMT < 8). **2**. Number of ensiform macrosetae on female metatarsus I: 0 = small (mean IMS = 8–15); 1 = large (mean IMS = 22–25). **3**. Number of teeth on retrolateral claw of female left tarsus IV: 0 = small (mean IVCTR < 2); 1 = moderate (mean IVCTR = 3–4); 2 = large (mean IVCTR > 6). **4**. Female metatarsus I: 0 = relatively short (mean IML/CL = 0.37–0.38); 1 = of moderate length (mean IML/CL = 0.40–0.48); 2 = relatively long (mean IML/CL = 0.55–0.56). **5**. Male tibia I prolateral mating setae: 0 = absent; 1 = present. **6**. Left arm of ICS base: 0





Figures 1, 2.—Diagrams comparing quantitative character values of *Atypoides* and *Antrodiaetus* species to demonstrate method used for coding quantitative characters. Horizontal bar represents the range, vertical bar the mean, and box the standard deviation (when $n > 4$). Sample size is given next to species name. Vertical dashed lines separate clusters of species with mean values significantly different ($P < 0.05$) from other such clusters; these are the character state boundaries. 1, Female IML/CL; 2, Male PTT/PTL.

= weak; 1 = strong and heavily sclerotized. **7**. Cheliceral apophysis: 0 = absent; 1 = well developed; 2 = vestigial. All *Antrodiaetus* males have an anterior-dorsal cheliceral prominence which, because of its position, is very probably a homologue of the cheliceral apophysis of *Atypoides* (Coyle 1971). We agree with Coyle (1971) that the high intra- and interspecific variability in the size and form of this prominence, and its small size in all species, support the hypothesis that it is a nonfunctional vestige of the cheliceral apophysis. Our coding represents this hypothesis. Coding the prominence as rudimentary (as state 1, intermediate between the well developed apophysis of *Atypoides* and the outgroup condition in which no sign of this structure is evident), does not alter the topology of the shortest trees, but it lengthens and increases the homoplasy of these shortest trees. **8**. ALS with: 0 = two articles; 1 = one article; 2 = absent. **9**. Spermathecal stalks: 0 = long; 1 = short. **10**. Dorsal profile of ICS tip (the left side of the terminal part of the ICS): 0 = concave; 1 = convex. **11**. Apex of OCS: 0 = on left side of ICS tip; 1 = on right side of ICS tip. **12**. OCS: 0 = narrow distally; 1 = broad distally. **13**. Anterior margin of bursa copulatrix: 0 = bilobed; 1 = not bilobed. **14**. Percent of male tibia I ventral retrolateral macrosetae which are ensiform: 0 = rarely > 30%; 1 = rarely < 40%. **15**. Percent of male tibia I prolateral macrosetae which are ensiform: 0 > 30%; 1 < 30%. **16**. Floor of bursa copulatrix: 0 = weakly sclerotized; 1 = with areas of moderate to heavy sclerotization. **17**. Male tibia I: 0 = considerably shorter than metatarsus I (mean ITL/IML = 0.71–0.81); 1 = slightly shorter than metatarsus I (mean ITL/IML = 0.85–0.99); 2 = slightly longer than metatarsus I (mean ITL/IML > 1.0). **18**. Male tibia I prolateral profile: 0 = more or less straight; 1 = strongly convex. **19**. Male tibia I ventral retrolateral macrosetae: 0 = scattered; 1 = clustered. **20**. Male metatarsus I distal macroseta: 0 = present; 1 = absent. **21**. Seta-less area on upper ectal surface of chelicera: 0 = present; 1 = absent. **22**. Male metatarsus I ventral retrolateral protuberance: 0 = absent; 1 = present. **23**. Spermathecal bowl: 0 = large and heavily sclerotized; 1 = small and weakly sclerotized. **24**. OCS surface sculpture: 0 = strongly file-like to serrate; 1 = smooth or weakly file-like. **25**. Male tibia I prolateral mating setae: 0 = large (macrosetae); 1 = small (bristles). **26**. Male palpal tibia in lateral view: 0 = thickest proximally; 1 = cylindrical; 2 = thickest distally. **27**. Male palpal tibia: 0 = relatively short and thick (mean PTT/PTL = 0.37–0.47); 1 = of moderate length and thickness (mean PTT/PTL = 0.31–0.33); 2 = relatively long and thin (mean PTT/PTL < 0.24). **28**. Sclerotization of OCS: 0 = weak to moderate; 1 = strong. **29**. Female metatarsus IV: 0 = relatively short (mean IVML/CL < 0.53); 1 = of moderate length

Table 2.—Data matrix used for cladistic analyses. See Methods section for character and character state descriptions. A hyphen indicates that a character is not applicable to that taxon and a question mark indicates that the character state is unknown.

Taxa	Characters and states												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Aliatypus	0&1	0&1	0	0	0	0	0	0	0	-	-	0	0
Al. gulosus	0	0	?	0	0	0	0	0	0	-	-	0	0
hypoth. ances.	0	0	1	0	0	0	0	0	0	-	-	0	0
At. hadros	1	0	1	0	1	0	1	1	1	0	0	1	0
At. riversi	0	1	2	2	0	0	1	1	0	0	0	1	0&1
At. gertschi	0	1	2	2	0	0	1	1	0	0	0	1	0&1
An. roretzi	1	0	1	1	1	1	2	2	0	0	0	1	0
An. pacificus	0	0	1	1	1	1	2	2	1	1	1	0	0&1
An. robustus	0	0	1	1	1	1	2	2	1	1	1	0	1
An. unicolor	0	0	1	1	1	1	2	2	1	1	1	0	1
An. occultus	?	?	?	?	1	1	2	2	?	1	1	0	?
An. yesoensis	1	0	1	1	1	1	2	2	1	1	1	0	1
An. cerberus	0	0	1	1	1	1	2	2	1	1	1	0	1
An. montanus	0	0	1	1	1	1	2	2	1	1	1	0	1
An. hageni	0	0	1	1	1	1	2	2	1	1	1	0	1
An. pugnax	0	0	1	1	1	1	2	2	1	1	1	0	1
An. lincolnianus	0	0	0	1	1	1	2	2	1	1	1	0	1
An. stygius	0	0	0	0	1	1	2	2	1	1	1	0	1
An. apachecus	0	0	0	1	1	1	2	2	1	1	1	0	1

(mean IVML/CL = 0.55–0.65); 2 = relatively long (mean IVML/CL > 0.67).

RESULTS AND DISCUSSION

Regardless of which outgroup was used, a branch and bound tree search followed by *a posteriori* weighting (using either the RI or RC) generated the same set of four shortest trees (Figs. 3, 4). These four trees differed only in the relationships among *An. pacificus*, *An. robustus*, and *An. unicolor*. All four trees contained a trichotomy involving *An. yesoensis*, *An. cerberus* and the *An. montanus* clade (clade 9 in Fig. 3). Re-weighting using the CI generated these same four trees plus four additional equally short trees identical in topology to the other four except that this trichotomy was resolved. All eight trees were shortest (length (TL) = 68, CI = 0.71, RI = 0.76, RC = 0.53) when using the hypothetical ancestral outgroup, longer (TL = 71, CI = 0.68, RI = 0.73, RC = 0.50) when *Aliatypus gulosus* was the outgroup, and even longer (TL = 77, CI = 0.71, RI = 0.74, RC = 0.53) when the genus *Aliatypus* was the outgroup.

The resolution of clade 9 generated by *a posteriori* weighting using the CI shows *An. cerberus* sharing with the *An. montanus* clade an ancestor that is not shared by *An. yesoensis*. However, this seems to be based on the weighting of the highly homoplastic character 20. Because of the high degree of polymorphism exhibited by this character, particularly in species with large sample sizes, and because *An. cerberus* and *An. yesoensis* are represented by small sample sizes, we consider this resolution to be dubious. The reduction of the seta-less area of the chelicera in some females of *An. cerberus* (Coyle 1971) may provide additional evidence that it and the *An. montanus* clade (which is united, in part, by the synapomorphic loss of the seta-less area in both sexes, character 21) share a recent common ancestor. However, we prefer to consider these relationships unresolved until more convincing evidence can be found to support a solution to the trichotomy.

The monophyly of the *An. lincolnianus* clade (clade 10) is strongly supported by characters 3 and 23–28 (Fig. 3). A sister species relationship between *An. stygius* and *An. apachecus* is supported by character 29. Monophyly of the *An. occultus* clade (clade 7) is supported by character 18. Clade 8 is supported by

Table 2.—Extended.

Characters and States															
14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
?	-	0	1	0	0	0	0	0	-	0&1	-	1&2	0&2	0	0&1
?	-	0	1	0	0	0	?	0	-	0	-	1	2	0	0
?	-	0	1	0	0	0	0	0	-	0	-	0	0	0	1
0	0	?	1	0	0	0	?	0	0	0	0	0	0	1	0
0	-	1	0	0	0	0	?	0	0	0	-	0	0	1	1
1	-	?	0	0	0	0	?	0	1	0	-	1	1	1	2
-	1	?	0	0	0	1	0	0	1	0	0	0	0	1	1
0	1	0&1	0	0	0	0&1	0	0	0	0	0	0	0	1	1
0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1
1	0	0	0	0	0	0&1	0	0	0	0	0	0	0	1	1
0	0	?	1	1	0	1	0	0	?	0	0	0	0	1	?
1	0	0	1	1	1	1	0	0	?	0	0	0	0	1	1
1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1
1	0	1	1	1	1	0&1	1	0	0	0	0	0	0	1	1
1	0	1	1	1	1	0	1	1	0	0	0	0	0	1	1
1	0	0&1	1	1	1	0	0&1	1	0	0	0	0	0	1	1
-	-	0	2	0	0	0	?	0	1	1	1	2	2	0	1
-	-	0	1	0	0	0&1	?	0	1	1	1	2	1	0	0
-	-	0	1	0	0	0&1	?	0	1	1	1	2	1	0	0

synapomorphy 19. Characters 16 and 21 support the monophyly of clade 9, the *An. montanus* clade. A sister species relationship between *An. hageni* and *An. pugnax* is supported by synapomorphy 22. The monophyly of clade 6 is weakly supported by character 17, which appears to have undergone a reversal in the progenitor of this clade. Clade 5 is weakly supported by characters 14–16. Character 14 could be interpreted as a synapomorphy of clade 8 with a parallelism in *An. unicolor* or as a synapomorphy of clade 5 with a reversal in *An. occultus*; both scenarios are equally parsimonious. Characters 15 and 16 both appear to be reversals to the outgroup condition. *Antrodiaetus roretzi* is clearly the most plesiomorphic species in the genus, with all other *Antrodiaetus* species forming a clade (clade 3) defined by characters 9–12, the last of which appears to involve a reversal. The monophyly of *Antrodiaetus* (clade 2) is strongly supported by synapomorphies 5–8. Coyle (1971) incorporated two of these synapomorphies (7, 8) in his phylogeny; we are proposing the other two (5, 6) for the first time. A sister species relationship between *At. riversi* and *At. gertschi* is well supported by characters 2–4. While characters 4 and 17 support the monophyly of clade 1, it should be noted that character 5 seems to contradict this resolution, supporting a sister relationship between *At. hadros* and *Antrodiaetus* to the exclusion of *At. riversi* plus *At. gertschi.*

Although relationships among *An. pacificus*, *An. robustus*, and clade 5 are ambiguous and cannot be resolved by this data matrix, there is evidence (albeit weak) to support our preferred phylogeny (Fig. 3). The vestigial male cheliceral apophysis is usually more prominent in *An. pacificus* than in other *Antrodiaetus* species (Coyle 1971), suggesting that this apophysis may have undergone further degeneration in the ancestor of all other North American *Antrodiaetus* species (clade 4). Also, the population of *An. pacificus* in eastern Washington, eastern Oregon and Idaho has a bilobed bursa copulatrix (character 13); this presumably ancestral condition is distinct from the unlobed condition of clade 4. We should also point out, however, that *An. robustus*, alone among the *Antrodiaetus* species, retains minute ALS vestiges (Coyle 1971), suggesting that loss of these spinnerets was not yet complete when this species diverged, and therefore that the lineage leading to this species may have originated earlier than *An.*

pacificus. Our preferred phylogeny (Fig. 3) requires a less complex biogeographic history that can be more easily correlated with known events than is the case for the other equally short trees (see below).

Our cladistic analyses have produced a phylogeny that is not only better resolved than Coyle's (1971, fig. 69) phylogeny, but significantly different in other ways. We have concluded that the three species of *Atypoides* (*sensu* Coyle 1968, 1971) probably comprise a paraphyletic group and that Coyle's *An. unicolor* species group (which included all *Antrodiaetus* species but *An. roretzi* and the three *An. lincolnianus* group species) is likewise paraphyletic. Our analyses support Coyle's hypotheses that *Antrodiaetus* is monophyletic, the *An. lincolnianus* group is monophyletic, and *An. stygius* and *An. apachecus* are sister species. They likewise support his contention that *An. roretzi* is a relict of a branch attached near the base of the *Atypoides* plus *Antrodiaetus* tree. We do not feel any urgency to formalize our hypothesis that *Atypoides* is paraphyletic. If further studies corroborate our findings, then *Atypoides* should be designated a junior synonym of *Antrodiaetus*.

BIOGEOGRAPHY

Mygalomorph spiders have been featured prominently among the few papers that have dealt with the historical biogeography of spiders (Pocock 1903; Raven 1980; Platnick 1981; Griswold 1991). Although early work on spider biogeography assumed that continents were stable and areas of high diversity were centers of origin (Pocock 1903), plate tectonics and cladistics have caused a drastic paradigm shift. Armed with an improved phylogeny, and knowledge and methodologies unavailable to Coyle in 1971, we should be able to improve upon his hypotheses about the biogeographic history of *Atypoides* and *Antrodiaetus*. Our biogeographic analysis proceeds from the model of vicariance biogeography as described by Croizat et al. (1974) and first applied to spiders by Platnick (1976). Briefly stated, we will presume that sister clades diverged from a common ancestor in response to a physical or ecological barrier which divided its range to prevent gene flow between the incipient sister taxa. We will also assume that clades evolved more or less in place.

All three species of *Atypoides* and 11 of the 13 *Antrodiaetus* species are endemic to North America (Coyle 1971). The North American species occupy three isolated provinces of endemism (Fig. 5): a western province containing *At. riversi*, *At. gertschi*, *An. pacificus*, *An. occultus*, *An. cerberus*, *An. montanus*, *An. pugnax* and *An. hageni*; an eastern province including *At. hadros*, *An. robustus*, *An. unicolor*, *An. lincolnianus* and *An. stygius*; and a southwestern province occupied solely by *An. apachecus*. The remaining two species, *An. roretzi* and *An. yesoensis*, are known only from the Japanese islands of Honshu and Hokkaido, respectively.

The *An. occultus* clade (Clade 7), with the exception of the Japanese species *An. yesoensis*, occurs only in the western province, and the *An. lincolnianus* clade (clade 10) is rooted in the eastern province. Thus, for all four candidate phylogenies (Figs. 3, 4), we can imagine the common ancestor of these two clades (the progenitor of clade 6) being split by a barrier into an eastern (*An. lincolnianus*) and a western (*An. occultus*) lineage. Later range expansions and vicariance events are required to explain the existence of *An. yesoensis* on Hokkaido and *An. apachecus* in Arizona and New Mexico. The other species in these two clades can be thought of as having differentiated as the result of more localized isolation.

In an attempt to resolve the ambiguous relationships among *An. pacificus*, *An. robustus*, and *An. unicolor*, we can evaluate the merits of our four competing phylogenies (Figs. 3, 4) by considering the biogeographic consequences of each. The trichotomy in Fig. 4a makes this cladogram uninformative regarding the biogeographic history of *An. pacificus*, *An. robustus*, and *An. unicolor*. The tree in Fig. 4b requires that an ancestral population would have to be divided into eastern and western taxa and then the western lineage would have to expand its range to the east and be divided again. All this would have to predate the origin of the *An. occultus* plus *An. lincolnianus* clade. The cladogram in Fig. 4c requires the same number of interprovincial range expansions and vicariance events, but the event that led to the divergence of *An. pacificus* and *An. robustus* need not have occurred before the rise of the *An. occultus* plus *An. lincolnianus* clade. Our preferred cladogram (Fig. 3) is biogeographically more par-

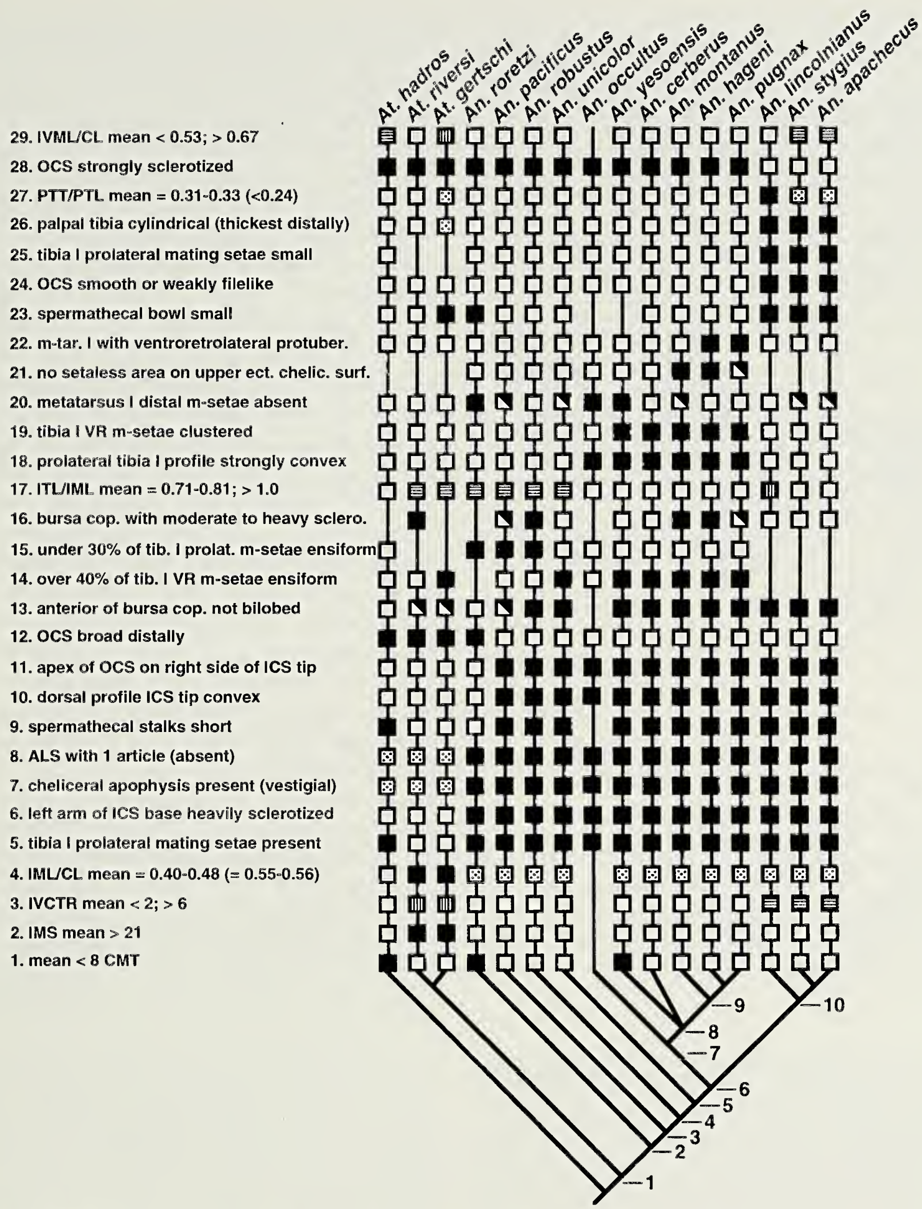


Figure 3.—Preferred cladogram of *Atypoides* and *Antrodiaetus* species. Numbers at nodes are used to identify clades discussed in the text. The plesiomorphic character state (i.e., the state of the hypothetical ancestral taxon) is denoted by a white box. For those characters (10, 11, 15, 23, and 25) where the outgroup state is unknown or not applicable, the state exhibited by *A. hadros* is denoted by a white box. Apomorphic states are described to the left of the cladogram and designated by patterned boxes. For binary characters, the apomorphic state is denoted by a black box. For triple-state characters where the two derived states are closer to each other than one of them is to the ancestral state, the intermediate state is described first and denoted by grey (stipples) and the extreme apomorphic state is described in parentheses and denoted by black. For triple-state characters where each derived state is closer to the ancestral state than to the other derived state, the first described state is designated by horizontal lines and the state following a semicolon is designated by vertical lines. Polymorphic taxa (exhibiting two or more states) are denoted by half white, half black boxes.

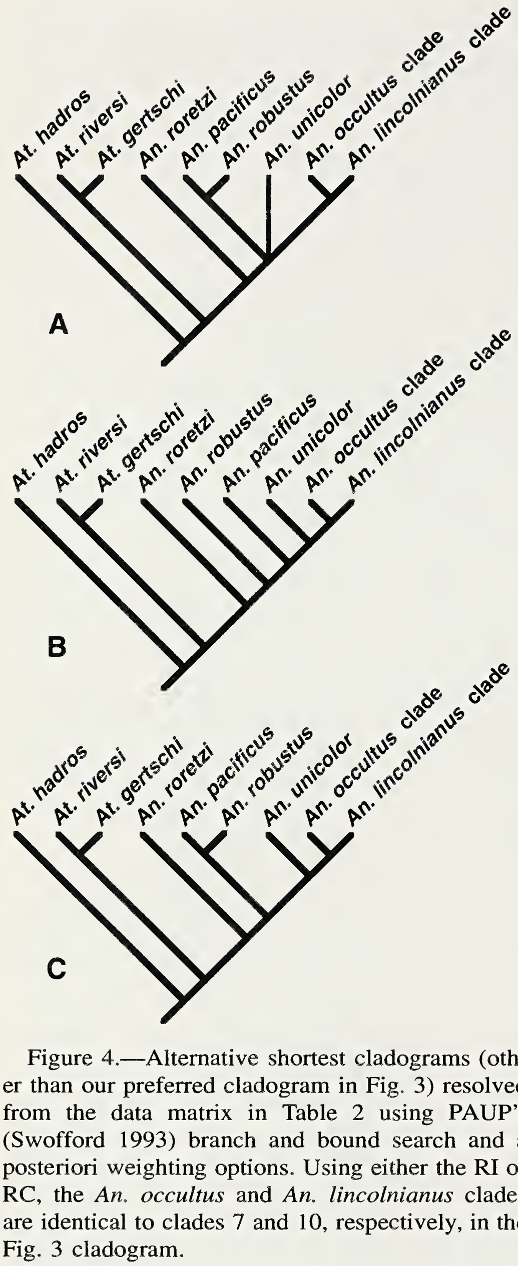


Figure 4.—Alternative shortest cladograms (other than our preferred cladogram in Fig. 3) resolved from the data matrix in Table 2 using PAUP's (Swofford 1993) branch and bound search and a posteriori weighting options. Using either the RI or RC, the *An. occultus* and *An. lincolnianus* clades are identical to clades 7 and 10, respectively, in the Fig. 3 cladogram.

simonious because it requires the fewest interprovincial range expansion events.

Proceeding from this preferred phylogeny, we will propose a scenario using known or suspected geological and ecological events which could have produced the observed distribution of *Antrodiaetus* species. The discovery of a fossil mygalomorph spider, *Cretacattyma raveni* Eskov & Zonshtein 1990, with a cheliceral apophysis (a unique synapomorphy for extant *Atypoides* and *Antrodiaetus*, character 7) in a lower Cretaceous deposit from Mongolia (Eskov & Zonshtein 1990), suggests that the *Atypoides* plus *Antrodiaetus* lineage arose before the Cretaceous. Despite tectonic plate reconstructions which indicate that Asia and North America were separated by a vast expanse of ocean until the end of the Cretaceous (Briggs 1987), evidence from plant and dinosaur fossils (Cox 1974; Cracraft 1974; Smiley 1976), and rafting terranes (Pielou 1979; Fujita & Newberry 1983) suggest the existence of upper Jurassic or lower Cretaceous faunal exchange between these regions. The terrane responsible for the uplift of the Verkhoyansk mountains in eastern Siberia is thought to have originated in western Laurasia and might have facilitated an exchange that could have permitted the presence of *Atypoides* and *Antrodiaetus* ancestors in both regions. We suggest that the precursor of *An. roretzi* may have been isolated from the common ancestor of all other *Antrodiaetus* species (clade 3) following just such a faunal exchange. Vicariance events generating the *At. hadros* lineage, the *At. riversi* plus *At. gertschi* lineage, and the *Antrodiaetus* lineage would have taken place in the North American portion of Laurasia and predated this event. Postulating such a great age for these events seems reasonable to us, not only from the evidence provided by *C. raveni* and other lower Cretaceous mygalomorph fossils (Eskov & Zonshtein 1990) but also from the discoveries of lower Cretaceous fossils of modern araneomorph spider families (Selden 1989, 1990) and from the hypotheses of Platnick (1976) and Griswold (1991) that Mesozoic vicariance events have created sister clades within extant spider genera.

The next important vicariance event in the history of the lineage, the isolation of the progenitor of *An. pacificus* from that of all other *Antrodiaetus* species (clade 4), may have been caused by the formation of the Mid-Continental Seaway separating eastern and western North America in the mid-Cretaceous (Cox 1974; Hallam 1979; Briggs 1987). By the beginning of the Tertiary, the Mid-Continental Seaway had receded (Cox 1974; Cracraft 1974), and during the early Tertiary, much of North America was covered by tropical to warm-temperate forests (Cracraft 1974). Under these conditions, the ancestor of clade 6

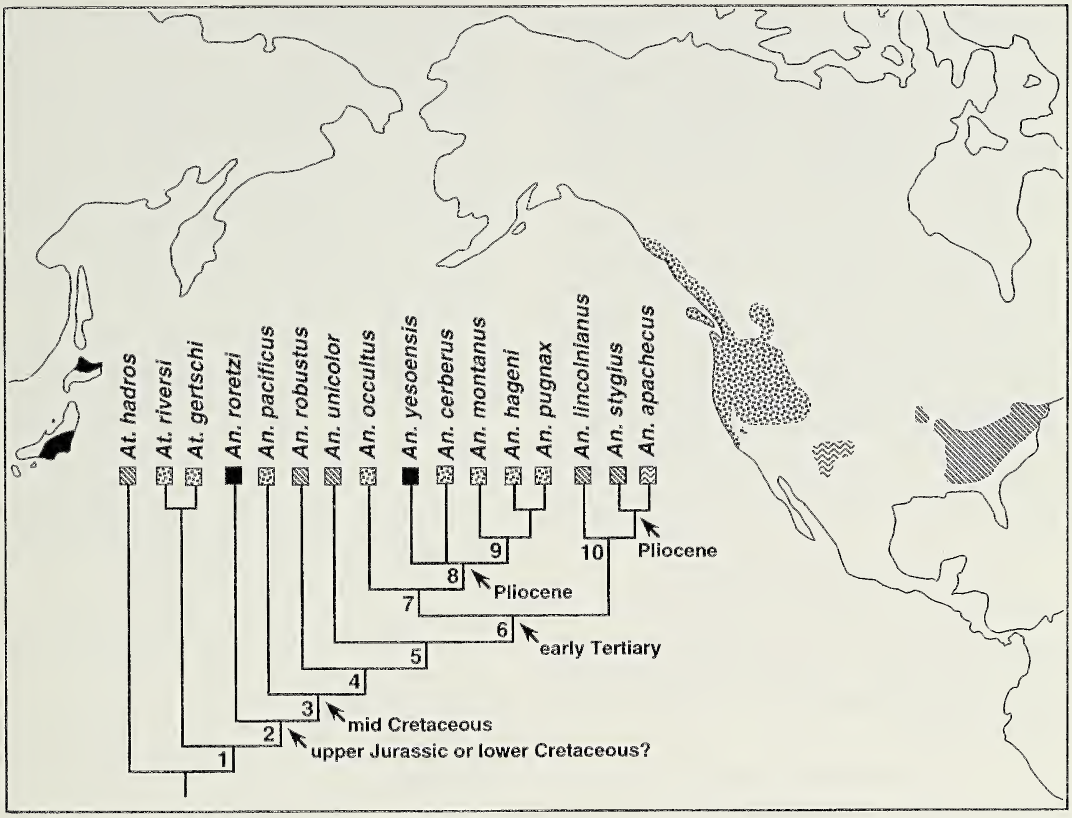


Figure 5.—Area cladogram of our preferred phylogeny with a map of North America and eastern Asia and showing the current world distribution of *Atypoides* and *Antrodiaetus* species. Four provinces of continuous or near continuous distribution are demarcated. All species are limited to one province. Box near species name signifies that species' province. Putative vicariance events discussed in the text which may have resulted in the divergence of clades are denoted by arrows and the names of the appropriate geologic period.

may have expanded its range westward across North America. The orogeny of the Rocky Mountains, beginning in the late Cretaceous and continuing into the Eocene (Pomerol 1982; Dott & Batten 1988), may have split this clade into western (clade 7) and eastern (clade 10) clades. The importance of the uplift of these mountains is supported by the current absence of antrodiaetid spiders from all but the southern-most outliers of the Rocky Mountains.

During the late Oligocene and mid-Miocene, a region of mixed mesophytic forest which connected the North Pacific from Oregon to Japan via a Bering land connection (Hopkins 1967) offered the last ecologically favorable opportunity for the expansion of *Antrodiaetus* into east Asia (Coyle 1971). (The more recent Pleistocene connection was unforested and its climate too harsh for *Antrodiaetus* [Coyle 1971].) The disappearance of this Tertiary link near the end of the Pliocene (Hopkins 1967) presumably isolated the ancestor of *An. yesoensis*. The remarkable physiographic and climatic fluctuations in the Pacific Northwest during the Pliocene and Pleistocene may have fostered the divergence of *An. montanus*, *An. pugnax*, *An. hageni* and *An. cerberus* (see Coyle 1971, p. 399). Land connections between Japan and the Asian mainland are believed to have developed periodically beginning in Mesozoic times and occurred as recently as the Pleistocene (Takai et al. 1963) and must be responsible for the existence of both *An. roretzi* and *An. yesoensis* on Japanese islands.

The western distribution of *An. apachecus* is probably the result of a range expansion by

the ancestor it shares with *An. stygius* into the southwestern part of the continent before the Pliocene, when climatic changes in central North America replaced the widespread forest with a broad semi-arid grassland that persists today as the Great Plains (Frey 1965; Coyle 1971).

There were numerous opportunities for faunistic exchange between eastern North America and Europe during both the Mesozoic and Cenozoic eras, and biogeographic evidence shows that many taxa used these routes. A temperate, forested land bridge apparently connected Europe with North America as late as the beginning of the Eocene (Cracraft 1974; Briggs 1987). It is unclear why *Antrodiaetus* failed either to disperse to or persist in Europe.

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SALTICIDAE OF THE PACIFIC ISLANDS. I. DISTRIBUTION OF TWELVE GENERA, WITH DESCRIPTIONS OF EIGHTEEN NEW SPECIES

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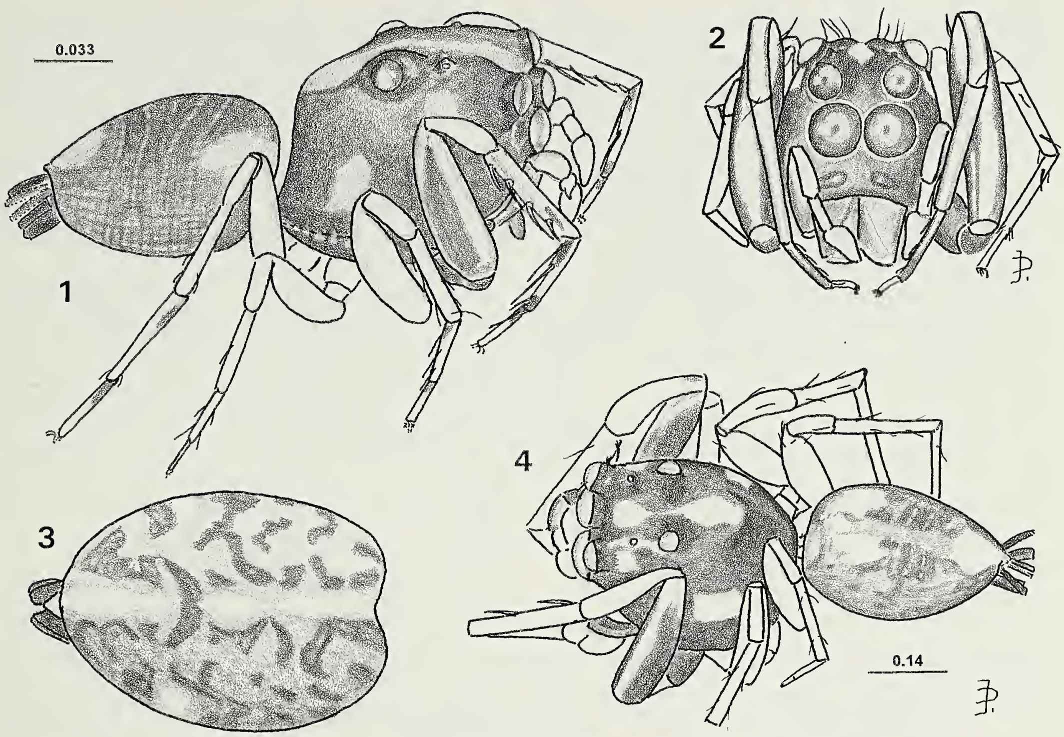
ABSTRACT. Pacific salticids of the genera *Athamas, Bianor, Efate, Ergane, Euophrys, Evarcha, Holoplatys, Myrmarachne, Omoedus, Palpelius, Phintella,* and *Zenodorus* are discussed. Eighteen new species are described: *Bianor obak, Bianor vitiensis, Efate fimbriatus, Efate raptor, Ergane carinata, Euophrys wanyan, Euophrys kororensis, Euophrys bryophila, Evarcha reiskindi, Holoplatys carolinensis, Myrmarachne edentata, Myrmarachne pisarskii, Myrmarachne edwardsi, Omoedus cordatus, Palpelius namosi, Palpelius trigyrus, Phintella planiceps,* and *Zenodorus ponapensis.* Illustrations and distribution records are presented for all new species. In the widespread species *Athamas whitmeei,* morphological variation on several islands is illustrated. *Efate albobicinctus* and *Zenodorus microphthalmus* are illustrated for comparison with newly described species.

Knowledge of spiders from the Pacific Islands extends back at least as far as Nieremberg (1635) which includes mention of spiders from the East Indies. Later, Walckenaer (1837) described spiders from the Mariana Islands, Celebes, Bismarck Archipelago and Tonga. In Die Arachniden Australiens, L. Koch (1871–1881) included a number of species that occur on the islands. Occasional data on Pacific species are scattered in many papers by various authors.

Until recently, intensive studies of Pacific spiders by spider specialists, or collections personally obtained by them, have been lacking. Most of the literature published from 1900–1950 has been the work of Berland (in numerous papers). Since 1950 there have been studies by Marples (1955a, 1955b, 1957, 1959a, 1959b, 1960, 1964), Chrysanthus (1958, 1959, 1960, 1961, 1963, 1964, 1965, 1967a, 1967b, 1968, 1971, 1975), Suman (1964, 1965, 1967, 1970), Levi (1967), Gertsch (1973), Lehtinen & Hippa (1979), Lehtinen & Saaristo (1980), Lehtinen (1981, 1993), Okuma (1987) Beatty & Berry (1988a, 1988b), Beatty et al. (1991), Berry (1987), Berry & Beatty (1989), Platnick (1993), Gillespie (1991, 1992, 1994), and Benton & Lehtinen (1995). Most of these have dealt primarily with spiders from the larger continental islands (Chrysanthus—New Guinea; Platnick—New Caledonia) or Hawaii (Gertsch; Gillespie; Suman), or with specific taxa (Suman; Gillespie; Lehtinen & Hippa; Lehtinen & Saaristo; Lehtinen; Beatty & Berry; Berry & Beatty; Beatty et al.). Data on the spider fauna of the oceanic islands remain relatively sparse.

This is the first of a series of papers dealing with the species of jumping spiders found on the Pacific Islands and the distribution patterns of those species on the islands. Except for Wanless's (1978) revision of the genus *Sobasina,* very little specifically on Pacific sal-



Figures 1–4.—*Athamas whitmeei* from Kusaie, Caroline Islands. 1, Lateral view of male; 2, Frontal aspect of male; 3, Abdominal pattern of female; 4, Dorsal view of male.

ticids has been published. However, records of various Pacific salticids are scattered among the papers cited above. Berland (1934) listed 40 salticid species from Polynesia. In later papers, which included other Pacific areas, he added 15 more. Marples described six new species from the Cook Islands, Tonga, Samoa and Fiji. The New Guinea fauna described by Chrysanthus overlaps the fauna of the smaller oceanic islands only in the case of cosmotropical or widespread Pacific species (e.g., *Bavia aericeps* Simon 1877, *Menemerus bivittatus* (Dufour 1831), and *Plexippus paykullii* (Aud. 1825)). A summary of the distribution of salticid species of the Pacific and Indonesian Islands, based both on literature and study of large collections, is given by Prószyński (in press).

The collections on which this paper is based were made primarily by James W. Berry, Elizabeth R. Berry, and Joseph A. Beatty (noted as JWB, ERB and JAB in the Material examined sections) in a series of collecting trips: Marshall Islands (1968, three months; 1969, three months); Palau (1973, six months); Guam, Yap, Truk, Ponape, Taiwan (1973, 1–2 weeks each); Yap (1980, six months); Marquesas, Tuamotu, Society, Cook and Fiji Islands (1987, six months total); and Hawaii (1995, one month). Specimens borrowed from the Bishop Museum (BPBM) and the American Museum of Natural History (AMNH) were also examined and are occasionally referred to. We treat here 22 species in 12 genera, of which 18 species are new.

We are aware that a few of the newly-described species do not fit comfortably in the genera to which they have been assigned. In the present state of salticid taxonomy, with over 400 genera (many of them essentially undefined) to consider, we can do no better. For this reason we have included brief descriptions of most genera. These descriptions apply only to the Pacific species of these genera and may or may not be correct for species from other regions. Diagnoses of genera are intended to distinguish only among genera reported from the Pacific Island region. Attempting to discriminate among all salticid genera of the world is a hopeless task in the current state of

taxonomy of the family. We define the Pacific region as including only Micronesia and Polynesia (including Fiji). The islands of Melanesia, the eastern Pacific, Philippines, Indonesia and vicinity of Australia and New Zealand are excluded. In the descriptions the genera are categorized by size as follows: small, 2–4 mm total length; medium, >4–8 mm; large, >8–16 mm; and very large, over 16 mm. The anterior, middle and posterior eye rows are referred to, respectively, as eyes I, eyes II, and eyes III. All measurements are in mm.

Simon (1901–1903) divided the salticids into unidentate, fissidentate and pluridentate groups of genera, but even he regarded this division as somewhat artificial. Recent workers (e. g., Davies & Żabka 1989) show increasing dissatisfaction with this arrangement. Numerous cases of apparent convergence in various characters that have been used taxonomically further complicate matters.

In salticids there are currently genera that differ in non-genitalic characters but have genitalia of the same form (e.g., *Harmochirus*—fissidentate, and *Bianor*—unidentate). Likewise, there are species of virtually identical somatic structure but with very different genitalia (e.g., *Coccorchestes* and an undescribed Pacific species provisionally assigned to *Sobasina*). Which set of characters should be considered more important for determining generic limits is currently moot.

Species limits in widespread Pacific genera also present a difficult problem. Among the three authors of this paper, there are differing opinions regarding whether each island or compact group of islands has endemic species in many genera. For that reason, we have used a broader species definition until intra-species variation in relation to inter-island variation of those species can be examined more closely.

To exemplify this treatment we present illustrations (Figs. 1–17) of variation in what we refer to as *Athamas whitmeei* from several islands. Initially these variants were treated as separate species; but, after examination of a number of specimens from each of several islands, we decided to leave them combined as a single species. There may be more than one species in this genus, but sufficient evidence for distinguishing them from each other does not exist currently.

Most of the salticid genera recorded from the Pacific occur also in Asia and/or Australia. Few genera, except for those that are cosmotropical, are common to the Pacific Islands and South America. Of the 42 genera recorded from Micronesia and Polynesia, 10 are restricted to the Pacific Islands (including, in this case, Melanesia). We treat two of these here (*Athamas* O. Pickard-Cambridge 1877 and *Efate* Berland 1938).

The holotype and other specimens of ***Euophrys bryophila*** new species are in the American Museum of Natural History (AMNH). Holotypes of the other new species will be deposited in the Bernice P. Bishop Museum (BPBM) (State Museum of Hawaii) in Honolulu. All adult specimens are paratypes unless specifically excluded in the text; juveniles are not paratypes.

Genus *Athamas* O. Pickard-Cambridge 1877

Discussion.—Members of the genus *Athamas* are widespread in the Pacific region, occurring from the western Caroline Islands to Henderson Island. Initially several species had been distinguished among our material on the basis of differences in size, color, length of the tibial apophysis of the male palp, clypeal height, number of spines of the male tibia I and slight variations in the palpal embolus and bulb. Examination of a number of specimens from each of several islands showed that most of these characters were highly variable on each island, especially size, coloration and male palpal apophysis. Figures 5–7 show some of the variations in epigyna, and Figs. 13–17 show the variations from island to island in the male palps. The number of tibial spines on the male first leg is correlated with the size of the spider and varies overall from 4–7 pairs. A range of 5–7 pairs was found in a few specimens from Kusaie, Caroline Islands.

The characteristics of tramp species appear to be well exemplified by *A. whitmeei*—abundance, wide distribution, a high level of variation and occurrence in marginal areas (e.g., Eniwetok, a relatively dry atoll on the north edge of the Pacific Island region). Localized speciation is not expected in tramp species because of their effective means of dispersal. Salticidae are known as reasonably effective ballooners (Salmon & Horner 1977).

Before recognizing a series of species in the genus a careful study of intra-population vari-

Map 1.—Major island groups of the Pacific Ocean. The three major divisions are (1) Micronesia, including the little islands in the western Pacific and generally north of the Equator (primarily the Caroline Islands, Mariana Islands, and the Marshall Islands), (2) Polynesia, forming a huge triangle in the central Pacific, with 17 different island groups (including Hawaii, Samoa, Tonga, Cook Islands, Society Islands and Marquesas), and (3) Melanesia, including Fiji and the islands to its west (excluding Indonesia).

ation for several island groups is required. It is entirely possible that more than one species does exist, but until we have stronger evidence we will not describe as species the variation in these spiders that we have seen from island to island.

Diagnosis.—This is an unusual salticid genus with an eye pattern clearly of the lyssomanine type (i.e., arranged in four rows, ALE positioned directly above AME), but the palpal organ is of the euophryine type (i.e., with the sperm duct looping inward (Figs. 15, 16) rather than being without convolutions (Figs. 27). The facial appearance is dominated by huge anterior median eyes (AME). The leg spination is also unusual: tibia I has 4–7 pairs of ventral spines, three of which are very long, metatarsus I with three pairs of long spines and tarsus I also with one pair of long spines. The cheliceral retromargin appears unidentate but has a minute second cusp on the side of the tooth nearer the base of the fang.

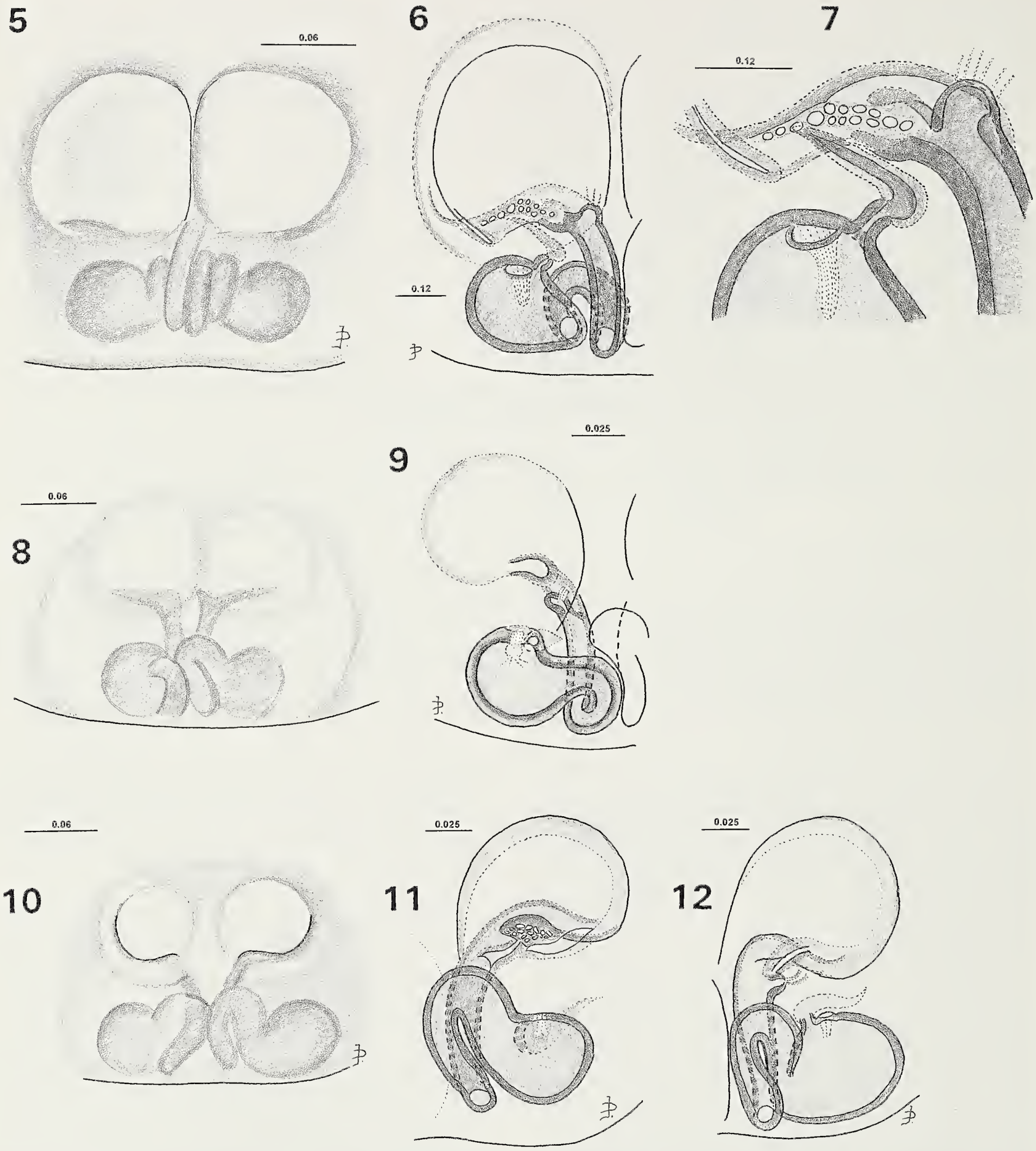
Athamas whitmeei O.P.-Cambridge 1877
Figs.1–17, Map 1

Athamas whitmeei O. P.-Cambridge 1877. Type from Samoa in Hope Entomol. Coll., Oxford University, Oxford, U.K., examined.

Athamas univittata Berland 1938. Female holotype from New Hebrides, Efate, Port Vila, June 1933, Risbec, in MNHN, Paris. First synonymized by Benton & Lehtinen 1995.

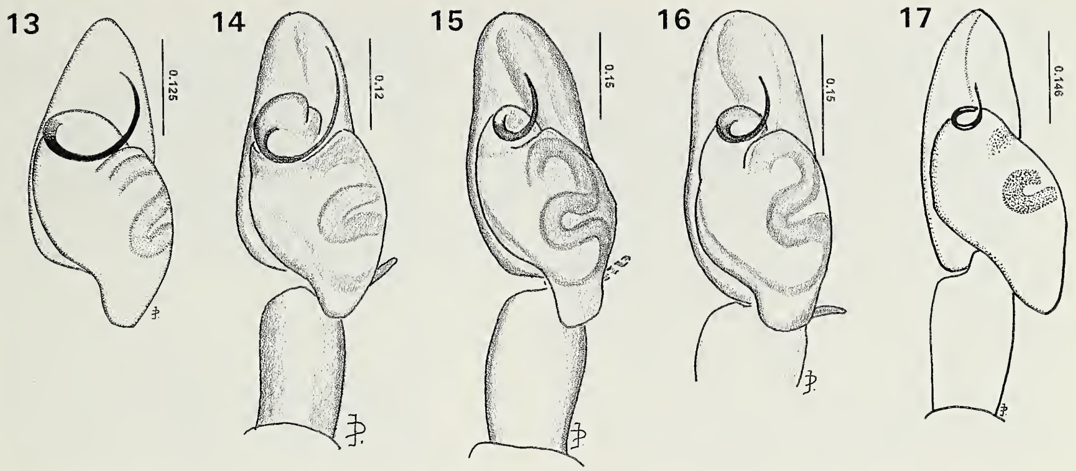
Discussion.—Berland distinguished *A. univittata* from *A. whitmeei* solely by the color pattern ("le dessin si particulier") of the unique female specimen. He cited the constancy of color pattern in *A. whitmeei* as justification for regarding *univittata* as a separate species ("donnée la grande fixité du dessin de *whitmeei*"). Without supporting evidence from other characters we are reluctant to recognize more than one species in the genus. Recently Jendrzejewska (1995) described four new *Athamas* species on the basis of one or two specimens each. No evidence concerning intrapopulation variation in any of the characters was presented. One species was based on a single specimen differentiated only by the absence of patches of white hairs on the carapace. These hairs are easily rubbed off, and their absence may be the result of handling. Additional information from DNA or protein analysis could show whether or not they are different.

Description.—*Male:* (n = 5). Total length



Figures 5–12.—Comparison of epigyna of *Athamas whitmeei* from various islands. 5–7. Female from Pulo Anna (Palau Islands); 5, Epigynum; 6, Internal structure of epigynum; 7, Details of copulatory ducts and pores; 8, 9, Epigynum of female from Kusaie (Caroline Islands) and internal structure showing single spermatheca and channels; 10, 11, Epigynum of female from American Samoa (Tutuila Island) and internal structure showing single spermatheca and channels; 12, Internal structure epigynum of female from Samoa, showing single spermatheca and ducts.

2.50–2.70 ($\bar{x}$ = 2.56), length of carapace 1.25–1.35 ($\bar{x}$ = 1.28), maximum carapace width 1.00–1.10 ($\bar{x}$ = 1.06), eye field length 0.65–0.90 ($\bar{x}$ = 0.78), eye row I width 0.70–0.75 ($\bar{x}$ = 0.73). Carapace dark brown with six patches of orange scales (white in long-preserved specimens): one in middle of eye field, another on the anterior, flat part of thorax, usually connected by a line of scales of various width; a pair of isolated spots just below eyes II, and another pair on sides of thorax anteriorly. Eyes large, clypeus height varies from 60–85% the diameter of AME. Two retrolateral cheliceral teeth, three prolateral



Figures 13–17.—Comparison of male palps of *Athamas whitmeei* from various Micronesian and Polynesian locations. 13, From Samoa Island, locality unknown (drawn by J. Prószyński in 1977, with permission from the WSRP, Siedlce, Poland); 14, From Pulo Anna Island in Palau (Caroline Islands); 15, From Tutuila (American Samoa); 16, From Kusaie (Caroline Islands); 17, From Tahiti (Society Islands) (drawn in 1980, with permission from WSRP, Siedlce, Poland).

cheliceral teeth. Abdomen heart-shaped, with two areas of bright orange scales. An oval spot in front of the spinnerets and a broad anterior area, sometimes divided, are black or dark grey. *Legs:* Leg formula 1-3-4-2; tibia-patella I length, 1.00–1.20 ($\bar{x}$ = 1.12); patella-tibia III ≥ IV. Males are characterized by the very long leg I, with particularly long femur and tibia, in preserved specimens usually bent and held close to face. *Palp:* Simple, with bulb produced proximad beyond cymbium, overlapping tibia. Tibial apophysis short-to-long, straight-to-slightly curved. Embolus arising from apex of bulb, curving counterclockwise, making about ¾ of a circle. Loop of embolus varying in diameter, length of embolus variable (Figs. 13–17).

Female: (n = 5). Total length 2.45–3.15 ($\bar{x}$ = 2.73), length of carapace 1.20–1.35 ($\bar{x}$ = 1.27), maximum carapace width 0.95–1.05 ($\bar{x}$ = 1.00), eye field length 0.65–0.80 ($\bar{x}$ = 0.73), eye row I width 0.70 ($\bar{x}$ = 0.70). Color pattern is a mosaic on both carapace and abdomen, consisting of a number of irregular, greyish or brownish grey spots on a pale background. The only contrasting element is a narrow, straight line of shining scales, orange (fresh) or white (preserved), which runs along carapace and abdomen, on the latter broken by dark spots in one or two places. Cheliceral teeth as in male. Shape of carapace and abdomen similar to male, but legs I and their segments are usually shorter. *Legs:* Leg formula 1-4-3-2, patella-tibia III ≥ IV. Patella-tibia I length 0.90–1.00 ($\bar{x}$ = 0.97). Ventral spines on tibia I usually five. *Epigynum:* Main diagnostic character is the epigynum with its internal structures. Epigynum with two anterior white membranous windows, round or oval, with sclerotized globular spermathecae and ducts visible behind them. Internal structures originate at the slit-like opening. First is a transverse membrane or lightly sclerotized duct running transversely along the posterior edge of the window. This duct carries a strange sieve-like structure at its internal wall consisting of apparently numerous minute openings. It passes into a sclerotized and thick-walled longitudinal duct, which has a distinct lateral swelling with transparent pores running from it. Longitudinal duct runs posteriorly and turns into a semicircular loop, of varying shape and diameter, which joins the spherical spermatheca. The spermatheca has distinct pores near its posterior cone. Membranous structures may be visible only when stained in Chlorazole Black E.

Material examined.—SOCIETY ISLANDS: *Tahiti*, 1884 (NHM Wien). "*Athamas whitmeei* Cbr. Samoa Isl.", 1♂, presumed to be one of the two syntypes, Coll. O. P.-Cambridge, Hope Entomol. Coll., Oxford Univ., Oxford, UK. **SAMOA**: *Salai-*

lus, W172:S14, 1♀, 20 May 1926 (E.H. Bryan) (AMNH). *Safune*, W172:S, 1♀, 14 May 1924 (E.H. Bryan) (AMNH). (The following specimens were collected by JWB, ERB and/or JAB; only islands and number of specimens are listed because of space limitations.) **CAROLINE ISLANDS**: *Palau Dist.*, 17♂28♀17imm.; *Yap*, 10♂14♀6imm.; *Ulithi*, 2♂3♀7imm.; *Truk*, 3♂9♀3imm.; *Ponape*, 2♂1♀8imm.; *Kusaie*, 2♂1♀1imm.; **MARSHALL ISLANDS**: *Eniwetok*, 1♂6♀2imm.; *Kwajalein*, 11♂11♀14imm.; *Majuro*, 15♂17♀14imm.; **FIJI ISLANDS**: *Viti Levu*, 1♂1♀2imm.; **AMERICAN SAMOA**: *Tutuila*, 2♂3♀4imm.; **SOCIETY ISLANDS**: *Moorea*, 1♀; **COOK ISLANDS**: *Aitutaki*, 3♂4♀3imm.; *Rarotonga*, 1♂3♀1imm.; **MARQUESAS ISLANDS**: *Fatu Hiva*, 1♂1♀; *Hiva Oa*, 2♂5♀3imm.; *Nuku Hiva* 9♂5♀3imm.

Distribution.—Fiji, Henderson, Mangareva, Niue, Samoa and the Austral, Caroline, Cook, Loyalty, Marshall, Marquesas, Society and Tokelau Islands.

Genus *Bianor* Peckham & Peckham 1885

Diagnosis.—Resembles *Harmochirus* Simon 1885 and *Modunda* Simon 1901 in genitalic characters and body form. Differs from *Harmochirus* by being unidentate rather than fissidentate. Differs from *Modunda* by having the carapace higher and broader at third eye row, ocular quadrangle wider behind than in front, flat surface of carapace ending abruptly behind posterior eyes and passing into the very steep posterior slope of the thorax. Bulb of male palp truncate, rather than rounded.

Descriptive notes.—Recognizable by central hood of the epigynum and the palpal organ, in which the bulb always seems to be truncated anteriorly, while more or less rounded in other related genera. Integument of carapace hardened with pitted surface, brown. Unidentate, with tibia I with three pairs of spines.

Bianor obak new species
Figs. 18–24, Map 2

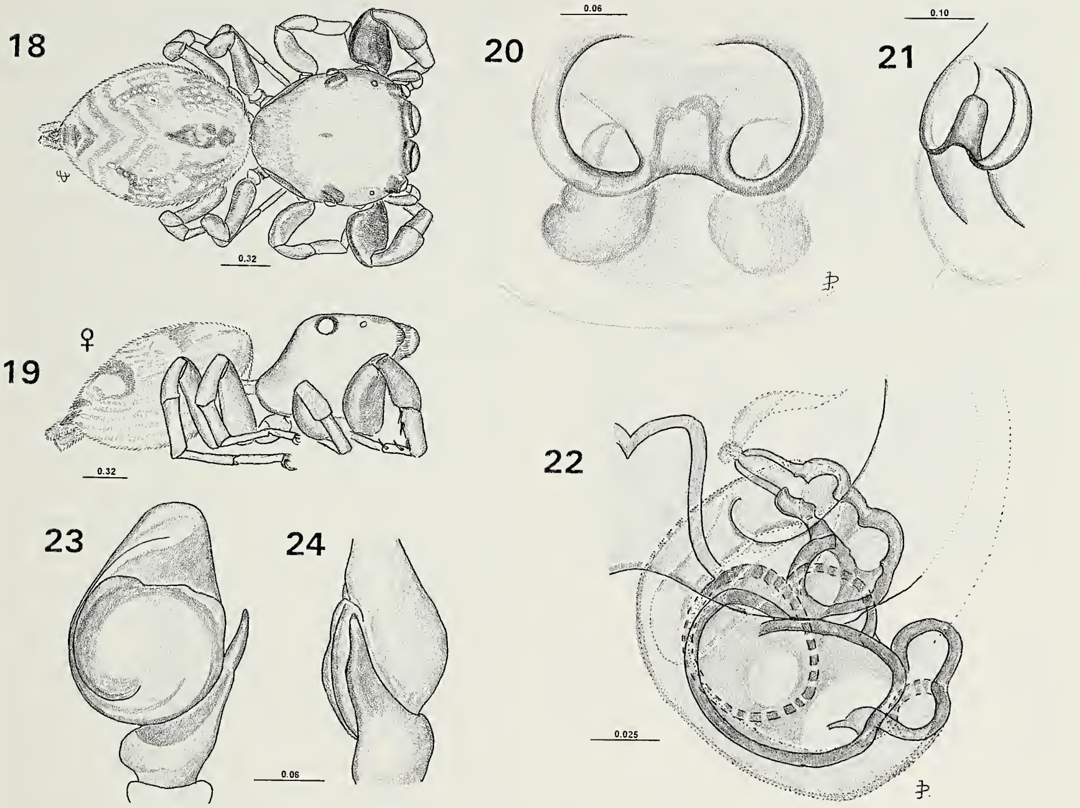
Holotype.—Female from Caroline Islands, Palau District, Peleliu Island, grass sweeping, 23 March 1973 (JWB & ERB) (BPBM).

Etymology.—The species name is a noun in apposition for the Obak, a chief on the island of Peleliu, where the type specimen was collected.

Diagnosis.—Setae surrounding eyes I in male entirely white. Anterior margin of palpal bulb truncate perpendicular to long axis of cymbium, embolus forming a circle. Palpal tibia shorter and tibial apophysis longer than in ***B. vitiensis*** new species. Female distinguished by course of internal epigynal ducts (Fig. 22).

Map 2.—Distribution of ***Bianor obak*** new species (★) in the Palau Islands and ***Bianor vitiensis*** new species (■) on Viti Levu in Fiji.

Description.—*Male:* (n = 5). There is considerable variation in size of specimens. Total length 2.6–3.3 ($\bar{x}$ = 2.90,), length of carapace 1.4–1.7 ($\bar{x}$ = 1.52), maximum carapace width 1.1–1.5 ($\bar{x}$ = 1.28), eye field length 0.8–1.0 ($\bar{x}$ = 0.94), eye row I width 0.9–1.2 ($\bar{x}$ = 1.08). Cephalothoracic integument dark chestnut brown with darkened area surrounding eyes III, covered with colorless thin adpressed scales, more intensely white scales form small white spots behind eyes III and a single median spot on posterior slope of the thorax; concentration of white scales along posterior part of the ventral rim of carapace. Abdomen brown with small anterior median dot of white scales, lateral whitish line around anterior half of abdomen at the edge of lateral surface, followed by two pairs of small white marginal round spots and very small and inconspicuous posterior whitish median chevrons; when dorsal setae become lost there appears a hardened dorsal integument, also brown. Frontal aspect brown, setae whitish, larger and more conspicuous than in ***Bianor vitiensis*** new species, setae surrounding eyes I entirely white; sparse longer setae overhanging cheliceral bases. Chelicerae brown, basally darker and with sparse white setae. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. Pedi-

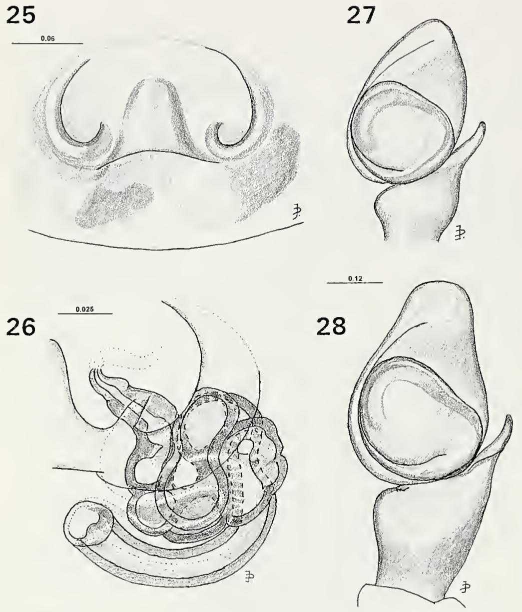


Figures 18–24.—***Bianor obak*** new species, from Palau. 18, Dorsal surface, female; 19, Lateral view, female; 20, Epigynum; 21, Epigynum in latero-ventral view; 22, Internal structure of epigynum showing right spermatheca and ducts; 23, Palpal organ ventrally; 24, Palpal organ laterally.

palps chestnut brown. *Legs:* Leg formula 1-4-3-2; patella-tibia I length 0.9–1.5 ($\bar{x}$ = 1.18), lengths of patella-tibia III and IV equal. Ventral spines of tibia I: outer row = 3, inner row = 3. Leg I darker chestnut brown, femora II-IV dark greyish brown, patellae and tibiae II-IV with single median lighter yellow ring, metatarsi II-IV yellow with darker joints, tarsi II-IV yellow.

Female: (n = 5). Total length 3.4–4.5 ($\bar{x}$ = 3.96,), length of carapace 1.7–1.8 ($\bar{x}$ = 1.74), maximum carapace width 1.4–1.6 ($\bar{x}$ = 1.50), eye field length 1.0–1.1 ($\bar{x}$ = 1.08), eye row I width 1.1–1.2 ($\bar{x}$ = 1.18). Eyes I surrounded with fawn setae except white on the ventral part of AME's rim and on external lateral rim of ALE's. Clypeus with white setae, short and dense, a few long whitish setae overhang chelicerae, anterior surface of chelicerae covered with long but sparse whitish setae. Body covered with adpressed whitish setae, thoracic slope almost vertical, begins immediately behind eye field. Carapace chestnut brown with darker lateral and anterior margins, scales on eye field colorless, more intensely white on thorax, slightly denser behind eyes III and above ventral edge of carapace. Cheliceral teeth as in male. Abdomen light brown with one pair of marginal white spots, surrounded by darker rims, and very indistinct lighter chevrons on posterior part of abdomen. *Legs:* Leg formula 1-4-3-2; patella-tibia I length 1.1–1.3 ($\bar{x}$ = 1.24), patella-tibia III shorter than IV. Ventral spines of tibia I as in male. *Epigynum:* With narrow hood, semicircular rims, and complexly coiled ducts (Figs. 20–22).

Material examined.–**CAROLINE ISLANDS**: *Palau*, Angaur, scrub forest, 3♀, 27 April 1973 (JWB & JAB). Malakal, under rocks in field, 4♀4imm, 17 April 1973 (JWB & JAB). Malakal, grass field, sweeping, 6♀4imm, 18 April 1973



Figures 25–28.—*Bianor vitiensis* new species, from Fiji: Viti Levu. 25, Epigynum; 26, Internal structure of epigynum showing right spermatheca and ducts; 27, 28. Palpal organ ventrally from two specimens in the same sample.

(JWB & JAB). Peleliu, Chief Obak's yard, grass sweeping, 7♂6♀(including holotype)4imm, 23 March 1973 (JWB & ERB).

Distribution.—Known from three islands in the Palau group of the Caroline Islands.

Bianor vitiensis new species
Figs. 25–28, Map 2

Holotype.—Female from Fiji: Viti Levu, Tholo-i-Suva Forest Park, sweeping and shaking trees, 6 May 1987 (ERB) (BPBM).

Etymology.—Named for the island of Viti Levu (Great Fiji) in Fiji, at present the only known location for this species.

Diagnosis.—In male, setae surrounding AME white ventrally, orange dorsally and laterally. Anterior margin of palpal bulb truncate oblique to long axis of cymbium, embolus forming a somewhat distorted oval. Tibia longer and tibial apophysis shorter than in ***B. obak*** new species. Female distinguished by internal epigynal ducts (Fig. 26). The width of the epigynal hood is variable and not diagnostic in this or the preceding species.

Description.—*Male:* (n = 5). Total length 3.4–5.4 ($\bar{x}$ = 3.98), length of carapace 1.6–2.2 ($\bar{x}$ = 1.82), maximum carapace width 1.4–2.1 ($\bar{x}$ = 1.64), eye field length 1.0–1.5 ($\bar{x}$ = 1.18), eye row I width 1.1–1.7 ($\bar{x}$ = 1.26). No distinct color pattern. Carapace uniformly chestnut brown, with darker pigmentation surrounding eyes III. Ventral edge of carapace black, with a single row of adpressed, whitish scales. Eye field finely pitted, shiny, with inconspicuous, adpressed, colorless minute scales, as well as with small upright sparse dark setae. Abdomen elongate oval, uniform light brown, inconspicuously darker marginally, covered with shiny, inconspicuous, transparent, adpressed scales and short upright bristles and even shorter setae, widely spaced. Face chestnut brown with very thin inconspicuous whitish setae, much thinner than in ***Bianor obak*** new species; however, setae around eyes and at the clypeal edge are broader and more conspicuous, those surrounding AME laterally and medially are orange, ventrally contrasting white, dorsally less conspicuous whitish mixed with yellow ones, those surrounding ALE similar but with yellow setae ventrally without contrasting white. Clypeus narrow with sparse, widely spaced whitish scales, a single row of whitish longer setae, widely spaced, overhangs cheliceral bases. Chelicerae light brown, with sparse whitish setae on basal half of their anterior surface. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. Pedipalps light greyish brown. *Legs:* Leg formula 1-4=3-2; patella-tibia I length 1.4–2.8 ($\bar{x}$ = 1.84), patella-tibia III and IV equal. Legs I are more intensely chestnut brown, legs II-IV light greyish brown with slightly darker femora, all segments without differentiated rings. Ventral spines of tibia I: outer row, 3; inner row, 3. Mouth parts, coxa I and sternum brown, coxae II-IV yellowish grey, abdomen grey with median area lighter.

Female: (n = 5). Total length 4.4–5.8 ($\bar{x}$ = 5.08), length of carapace 1.7–2.2 ($\bar{x}$ = 1.96), maximum carapace width 1.7–1.9 ($\bar{x}$ = 1.82), eye field length 1.0–1.4 ($\bar{x}$ = 1.24), eye row I width 1.2–1.4 ($\bar{x}$ = 1.34). Carapace uniform dark chestnut brown, with only surroundings of eyes III and anterior edge darker pigmented, covered with short, adpressed white setae. Abdomen appears almost uniformly brownish or brownish-grey, with indistinct whitish setae. An indistinct pattern is seen in some specimens, of 2–3 lighter, whitish, diagonal lines

marginally, a median line of small whitish chevrons in the posterior half, and a darker median line along anterior half of abdomen. Lacks the pair (or pairs) of small dark-edged marginal white spots, which seem to be characteristic of *Bianor obak.* Dense band of white setae on clypeus delimits oval orange area on which eyes I are located, AME surrounded by orange and a few single white setae ventrally, ALE also surrounded by orange with a few white setae dorsally; there is a row of sparse white setae at the clypeus edge, overhanging cheliceral bases. Chelicerae brown with sparse whitish setae; pedipalps yellow with white setae. *Legs:* Leg formula 4-1=3-2; patella-tibia I length 1.2–1.8 ($\bar{x}$ = 1.56), patella-tibia III and IV equal. Legs I brown. Legs II-IV brownish-greyish-yellow. Ventral side light brown, with mouth parts and sternum darker brown. Epigynum and its internal structure are shown in Figs. 25, 26.

Material examined.—FIJI: *Viti Levu*, Namosi Dist., hill forest on Namosi road, about 7 km N of Queen's Rd., 19 May 1987, 2♀,(JWB & ERB). 3.4 km N of Queen's Road on Namosi Road, grassy meadow by stream, sweeping, 1♂4♀7imm, 7 May 1987 (JWB & ERB). 5 km E of Komave village, in coral rubble on beach, 1♀1imm, 24 May 1987 (JWB & ERB). Nandarivatu, pine/scrub forest beside guesthouse, sweeping/shaking, elev. 800 m, 1♀, 14 May 1987 (JWB & ERB). Nandarivatu, forestry station, sweeping, 1♀4imm, 12 April 1987 (JWB & ERB). 8–10 mi by King's Road N of Nausori, hill forest, on vegetation, 1♀, 19 May 1980 (JAB). 1.7 km S of Naimborembore (near Nausori), 1♀, 8 May 1987 (JAB). Hill forest about 8 miles NE of Navua, tree shaking, 1♀1imm, 2 May 1987 (JWB & ERB). Nausori, from shaking banana leaves, 7♂7♀10imm, 18 May 1987 (JWB & ERB). Tholo-I-Suva Forest Park, shaking & sweeping trees, 1♀ (holotype), 6 May 1987 (ERB). Nine km W of Suva, (W of Lami), cut over forest, 1♂1♀2imm, 23 May 1987 (JWB & ERB).

Distribution.–Known only from Viti Levu in Fiji.

Genus *Efate* Berland 1938

Discussion. The genus *Efate* was established by Berland (1938) for the single species *E. albobicinctus* from the New Hebrides (now Vanuatu), which was also later reported from Samoa (Marples 1955). Two additional species are described here.

Diagnosis.—Small-to-medium ant-like fissidentate salticids. The only similar genera in the Pacific are *Rarahu* Berland 1929 and *Sobasina* Simon 1897. *Rarahu* differs from *Efate* by having leg spines only on metatarsus I. The male palp of *Efate* is of the euophryine type (Fig. 38), that of *Sobasina* is not. In the *Efate* epigynum the openings are widely separated (by more than their diameter) and the ducts short (Figs. 36, 37), *Sobasina* has openings close together and ducts long.

Descriptive notes.—Ant-like species of rather uniform appearance about 3–5 mm long. Carapace flattened, low, eye field occupying half of its length, lateral eyes on the edge of carapace, posterior eyes protruding somewhat. Eye field finely rough and shiny, covered with sparse, minute, colorless adpressed setae. An indistinct line of whitish setae behind eye field and a patch of longer whitish setae at the rear thoracic margin, on each side of the pedicel. Pedicel short but readily visible from above. Abdomen long, narrower than carapace, broadest just behind the middle, then narrowing posteriorly. Color pattern variable, either two white transverse lines on dark background or some light and dark areas, transverse areas or lines, related to that pattern. Clypeus obsolete, chelicerae small, their length equal to diameter of AME, broad, anterior surface flattened with distinct antero-lateral edge. Promarginal teeth two, basal one small, triangular, distal one wide and 3–4 cusped; retromarginal tooth fissidentate. *Legs:* Legs I have femur and tibia + patella enlarged, with tibia in some forms more strongly developed, compressed and swollen ventrally (more pronounced in females), but in males of *E. albobicinctus* not swollen. Tibia with 5–6 pairs of ventral spines; there is usually a ventral crest of two or more rows of long flattened dark setae, also not developed in males of some species (*E. albobicinctus*). *Palp:* Of generalized euophryine type with oval, moderately broad bulb, medium length tibial apophysis and shortened embolus, largely hidden dorsally to bulb, with only end of tip visible. *Epigynum:* With a pair of round openings, usually widely separated, leading to short ducts which open into nearly spherical seminal receptacles. A bell-shaped hood between openings except in *E. raptor* new species.

Efate albobicinctus Berland 1938
Figs. 29–35, Map 3

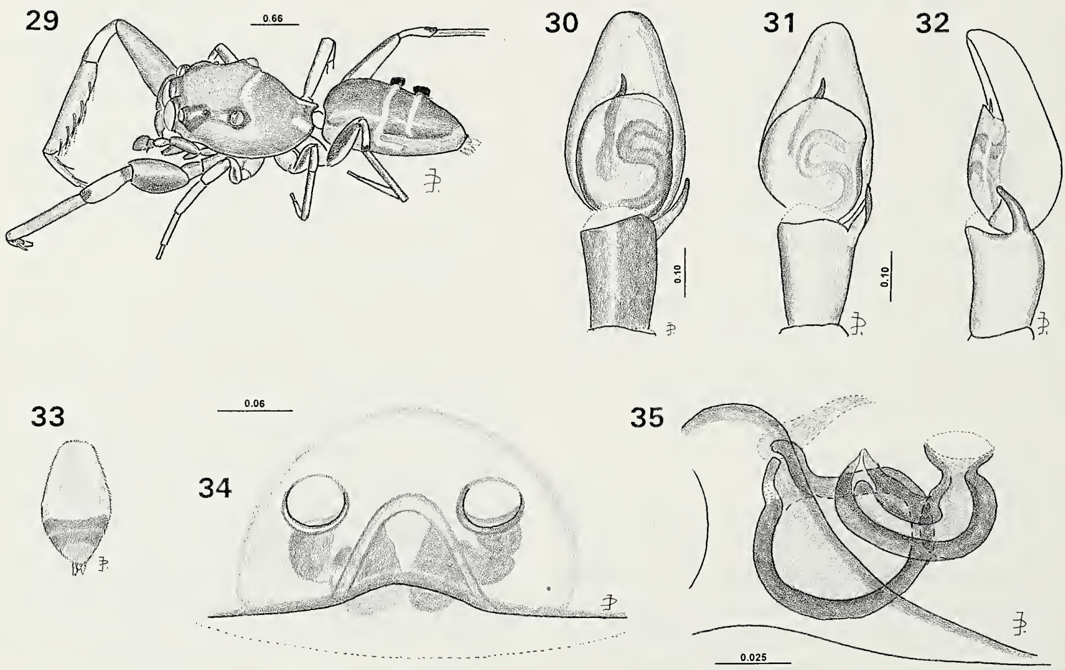
Efate albobicinctus Berland 1938.

Holotype.—Male from New Hebrides, Efa-

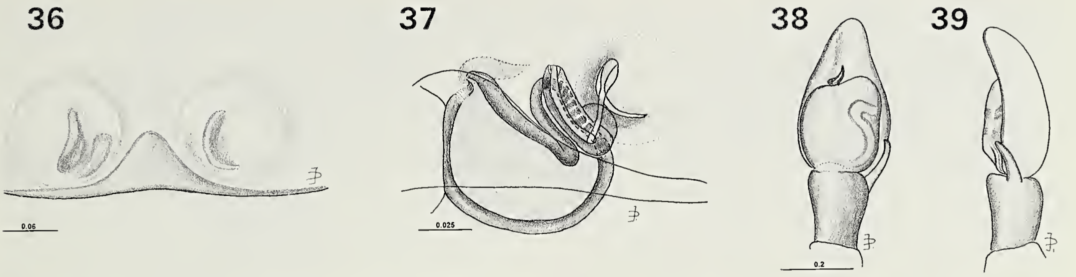
Map 3.—Distribution of *Efate albobicinctus* (★), ***Efate fimbriatus*** new species (■), and ***Efate raptor*** new species (□).

te, Apr.-May 1934, Coll. Aubert de la Rue, in MNHN, Paris, not seen.

Description.—*Male*: (n = 5). Total length 3.5–4.2 ($\bar{x}$ = 3.72), length of carapace 1.6–2.0 ($\bar{x}$ = 1.78), maximum carapace width 1.1–2.0 ($\bar{x}$ = 1.56), eye field length 1.0–1.1 ($\bar{x}$ = 1.04), eye row I width 1.0–1.2 ($\bar{x}$ = 1.12). Carapace dark brown, with lighter reddish brown band behind eye field. Abdomen with dark greyish brown scutum (only in this species of the genus) and striped grey sides. Spinnerets yellowish. Face dark brown; chelicerae brown. Pedipalps darker brown, legs I brown with patella and tarsus light yellow. Mouth parts, coxa I and trochanter I brown, sternum brown, darker marginally, coxae and trochanters II-IV light yellow, abdomen ventrally uniform dark greyish-brown. *Legs:* Leg formula 1-4-3-2; patella-tibia I length 1.4–2.0 ($\bar{x}$ = 1.60), patella-tibia III shorter than IV. Legs I with coxa, trochanter and femur dark brown, patella yellow, dorsally with dark brownish-grey basal end and apical spot; tibia I light brown with a spot of whitish setae prolatero-dorsally near apical end, with five pairs of ventral spines, but no ventral crest of setae; tibia cylindrical, slightly compressed; metatarsus dorsally light brown, laterally darker brown, with three pairs of long ventral spines, tarsus yellow. Legs II-IV yellow, with dark brown prolateral surfaces of femora II-III,



Figures 29–35.—*Efate albobicinctus*. 29, General appearance of male; 30, Palpal organ ventrally of male from Ponape; 31, Palpal organ ventrally of male from Ponape; 32, Palpal organ of male from Fiji; 33, Abdominal pattern of male from Fiji; 34, Epigynum of female from Fiji; 35, Internal structure of epigynum showing single spermatheca and ducts, from Fiji.



Figures 36–39.—***Efate fimbriatus*** new species. 36, Epigynum, female from Caroline Islands; 37, Internal structure of epigynum of female from Caroline Islands; 38, Palpal organ ventrally from Caroline Islands; 39, Palpal organ, laterally, from Marshall Islands.

prominent dark brown lines prolaterally along tibiae II-IV, two dark spots prolaterally on patellae II-IV and a dark spot apically on dorsal surface of patella IV; there are dark lines retrolaterally on tibia IV (prominent), metatarsus IV (indistinct) and on femur II (thin, in basal part only). *Palp:* Embolus short, palp virtually indistinguishable from ***E. fimbriatus*** new species; see Figs. 30–32.

Female: (n = 3). Total length 4.5–4.7 ($\bar{x}$ = 4.60), length of carapace 1.9–2.0 ($\bar{x}$ = 1.93), maximum carapace width 1.2 ($\bar{x}$ = 1.20), eye field length 1.1–1.2 ($\bar{x}$ = 1.13), eye row I width 1.1–1.2 ($\bar{x}$ = 1.17). Carapace yellow with eye field anteriorly darker; line of whitish setae behind eye field and hind marginal spots more obvious than in male. Abdomen anteriorly light, whitish, posterior third of abdomen, behind second white line, grey. Spinnerets whitish. Face and chelicerae light chestnut brown; pedipalps yellow. Mouth parts light brown to yellowish-brown, sternum whitish-yellow, coxae and trochanters I-IV whitish, abdomen whitish. *Legs:* Leg formula 4-1-3-2; patella-tibia I length 1.4 (n = 1), patella-tibia III shorter than IV. Femur and tibia laterally yellowish light brown, patella and apical end of tibia I whitish, metatarsus and tarsus yellow. Leg I femur yellow, patella whitish, tibia brownish-yellow, apically with whitish ring, with five pairs of ventral spines and ventral crest of setae, width of tibia I 40% of its length; metatarsus yellow with three pairs of long ventral spines, tarsus yellow. Legs II-IV whitish, with greyish pigmented line apically on prolateral surface of femur IV. Prolateral surfaces of femur III and tibia IV yellow; remaining segments whitish. *Epigynum:* hood short but narrower than in ***E. fimbriatus*** new species, extends over half of each spermatheca, curve of sclerotized duct developed more posteriorly, spermatheca globular and smaller than in *E. fimbriata* (Figs. 34, 35).

Material examined.—**CAROLINE ISLANDS**: *Ponape*, Kolonia, in building, 1♂, 28 March 1980 (JAB). Kolonia, on and in buildings, 1♂, 27 March 1980 (JAB). East of Kolonia palm forest, elev. 200 ft., 2♂1imm., 5 June 1973 (JAB & JWB). Kolonia, 1♂1♀, 3 June 1950 (P.A. Adams) (BPBM). Jokej, 1♀1imm, 10 January 1953 (J.F.G. Clarke) (BPBM). *Yap*, Fedor Village, forest, tree shaking, 3♂, 31 January 1980 (JWB). Gilman, coconut undergrowth, 1♂, 29 May 1973. (JAB & JWB). *Truk*, Moen Is., mixed forest above quarry, shaken from trees, 3♂9♀17imm., 12 June 1973 (JAB & JWB). Moen, S Slope of Mt. Tonaachau, 1♀, 2 April 1949 (R.W.L. Potts) (BPBM). *Kusaie*, Hill 750, 230 m, 1♀, 25 February 1953 (J.F.G. Clarke) (BPBM). **FIJI**: *Viti Levu*, N of Singatoka, sweeping & shaking along river, 3♂1♀21imm., 21 May 1987 (JWB & ERB). Near Mbau, under stones and swept on dry slope, 5♂3♀4imm, 9 July 1958 (B.J. Marples). Ovalau, Wai-ni-loka, 2♀, 11 July 1938 (L. Berland) (BPBM). **MARIANA ISLANDS**: *Guam*, Mt. Alifan, 1♀, August 1952 (N.L.H. Krauss)(BPBM). **NEW HEBRIDES**: *Santo I.*, Big Bay, elev. 0–30 m, 5♂, 16 September 1979 (W.C. Gagne) (BPBM). **SOLOMON ISLANDS**: *Tulagi*, 1♀, 17 July 1934 (BMNH).

Distribution.—New Hebrides, Caroline Islands, Guam, Fiji.

Efate fimbriatus new species
Figs. 36–39, Map 3

Holotype.—Male from Marshall Islands, Kwajalein Atoll, Gugeegu Island, shaken from trees, 24 July 1969 (JWB) (BPBM).

Etymology.—The name *fimbriatus*, fringed, refers to the presence of the ventral fringe of dark setae on the first tibia in both sexes of this species.

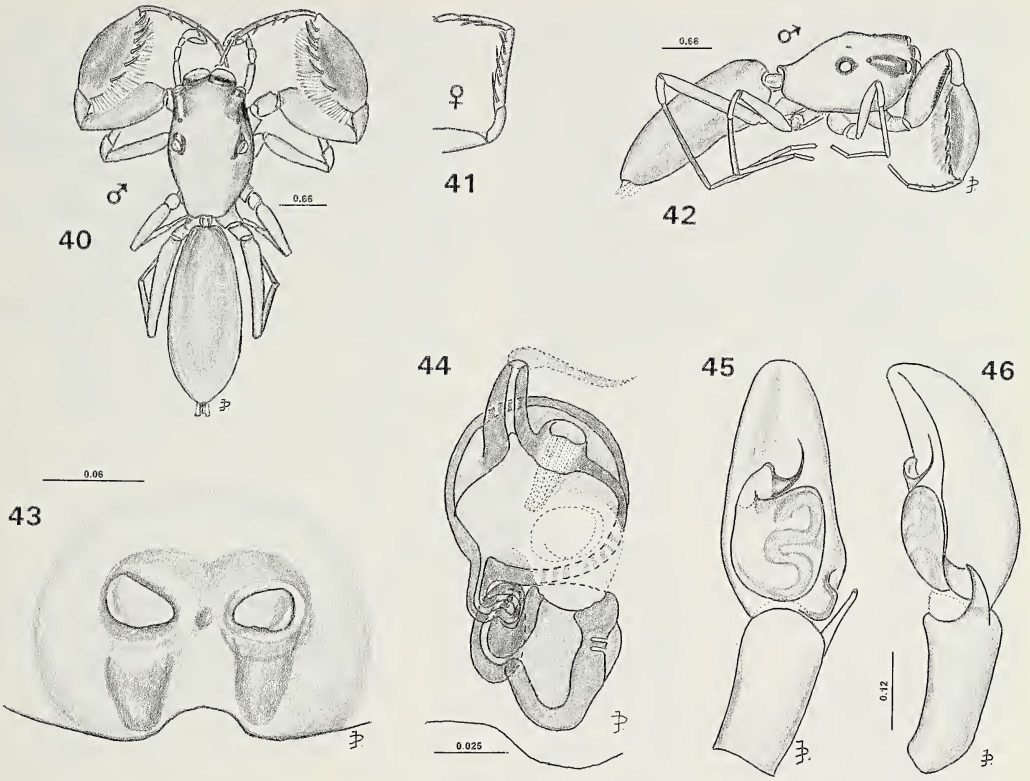
Diagnosis.—Differs from the other two species of the genus by proportions of epigynum and palpal organ (Figs. 36–39); tibia I compressed and with ventral setal crest in both sexes, color pattern light.

Description.—*Male*: (n = 3). Total length 3.6–4.8 ($\bar{x}$ = 4.37), length of carapace 1.8–2.4 ($\bar{x}$ = 2.20), maximum carapace width 1.1–1.6 ($\bar{x}$ = 1.43), eye field length 1.0–1.4 ($\bar{x}$ = 1.13), eye row I width 1.1–1.5 ($\bar{x}$ = 1.33). Carapace light brown, posteriorly lighter, eye field darker brown, with a small oval depression in the foveal area and more prominent bulge just behind it, remnants of line of white setae behind eye field practically invisible. Abdomen with soft integument, olive grey in preservative, anteriorly lighter, with anterior line of white setae obvious but not contrasting. Posterior with indistinct white line in the form of a sparse row of whitish setae, abdomen covered with short brown setae, spinnerets whitish. Face fawn; chelicerae yellowish-fawn. Pedipalps with femur greyish-brown, patella, mouth parts, coxa I and trochanter I brownish yellow, sternum greyish-yellow marginally, coxae and trochanters II-IV whitish, abdomen ventrally uniform light greyish-olive. *Legs:* Leg formula 1-4-3=2; patella-tibia I length 1.6–2.8 ($\bar{x}$ = 2.27), patella-tibia III shorter than IV. Legs I light brown with whitish spots laterally on patella and apically on tibia I, metatarsus dorsally whitish-yellow, laterally darker yellow, tarsus whitish-yellow. Leg I coxa, trochanter, femur, patella and tibia brownish-yellow, patella with whitish spot prolaterally; tibia I apically with narrow whitish ring, with five pairs of ventral spines and ventral crest of greyish setae, width of tibia about 33% of length of segment; metatarsus laterally brownish-yellow, dorsally and ventrally whitish, tarsus I whitish. Legs II-IV whitish, with brown prolateral surface of femur IV, femora II-III with a prolateral brown line; thinner prolateral brown lines run along tibiae II-IV and retrolaterally on tibia IV. Also a weak dark spot apically on patella IV; remaining segments whitish. *Palp:* Tibia greyish-yellow, cymbium light fawn with whitish anterior part; loop of the seminal receptacle in bulb tighter, narrower (Figs. 38, 39).

Female: (n = 4). Total length 4.2–5.0 ($\bar{x}$ = 4.60), length of carapace 2.0–2.2 ($\bar{x}$ = 2.08), maximum carapace width 1.2–1.4 ($\bar{x}$ = 1.30), eye field length 1.1–1.2 ($\bar{x}$ = 1.15), eye row I width 1.2–1.3 ($\bar{x}$ = 1.25). Larger than male, more similar to male of *E. albobicinctus*. Carapace uniform brown, a line of white setae behind eye field and white spots at thoracic hindmargin. Abdomen with soft integument, posteriorly brownish-grey, antero-medially yellowish-grey, with anterior whitish line barely visible, the posterior white line sometimes not visible; abdomen covered with short and very sparse colorless setae. Spinnerets whitish. Face chestnut brown; chelicerae brownish; pedipalps greyish-brown with lighter tip of the tarsus; legs I light brown with lighter apical end of tibia I, metatarsus and tarsus light brownish-yellow. Mouth parts, coxa I and trochanter I brownish-yellow, sternum brown, coxae and trochanters II-IV whitish, abdomen ventrally uniform light grey with olive hue. *Legs:* Leg formula 4=1-3-2; patella-tibia I length 1.6–1.8 ($\bar{x}$ = 1.68), patella-tibia III shorter than IV. Leg I coxa, trochanter, femur, patella and tibia light brown, patella with indistinct lighter spot prolaterally; tibia I apically with narrow whitish yellow ring, with five pairs of ventral spines and ventral crest of greyish flattened setae; tibia I width 37% of its length; metatarsus light brownish-yellow, with three pairs of long ventral spines; tarsus yellow. Legs II-IV whitish, with brown prolateral surface of femora III-IV, prolateral brown line on femur II; thinner prolateral brown lines run along tibiae II-IV and retrolaterally on tibia IV; also a weak dark spot apically on patella IV; remaining segments whitish. *Epigynum:* hood short and broad, extends over the whole spermathecae, bend of sclerotized channel developed rather anteriorly, spermatheca more transverse oval and broader than in remaining species (Figs. 36, 37).

Material examined.—**CAROLINE ISLANDS**: *Kusaie*, Lelu I., beating, 100 m, 1♂1♀, 12 March 1953 (J.F.G. Clarke)(BPBM). **MARSHALL ISLANDS**: *Kwajalein Atoll*, Gugeegu Island, shaken from trees, 1♂(holotype)1♀3imm, 24 July 1969 (JWB). *Majuro Atoll*, Majuro Isl., shaken from trees coconut-breadfruit community, 2♂2♀6imm., 2 August 1969 (JWB). Arniel Island, shaken from trees in coconut-*Pandanus* forest, 1♀1imm., 1 August 1969 (JWB).

Distribution.—Known only from the Caroline and Marshall Islands.



Figures 40–46.—***Efate raptor*** new species, from Fiji. 40, Dorsal appearance of male; 41, Tibia of female; 42, Lateral appearance of male; 43, Epigynum; 44, Internal structure of epigynum showing right spermatheca and ducts; 45, Palpal organ, ventrally; 46, Palpal organ, laterally.

Efate raptor new species
Figs. 40–46, Map 3

Holotype.—Male from Fiji, Viti Levu, Lami on tree in field 23 May 1987 (JWB & ERB) (BPBM).

Etymology.—The name is a noun in apposition based on the raptorial appearance of the first legs of the male.

Diagnosis.–The raptorial appearance of the first legs, fringe of setae on first tibia and long embolus distinguish the male. In the female the slender first tibia without setal fringe and the position of the epigynal openings ventral to the spermathecae rather than lateral to them are distinctive.

Description.—Both sexes similarly shaped. Abdomen elongate oval. Carapace with eye field flat, posterior slope begins shortly behind, no thoracic constriction. Rugosity of eye field so minute as to be practically invisible, profile of carapace slightly different from other species, with thoracic slope beginning just behind the eye field, without any intermediate depression, and sloping diagonally, gently and without any incipient bulge; no transverse lines of whitish setae nor whitish spots at the end of thorax. Pedicel short.

Male: (n = 2). Total length 3.8, 4.5; length of carapace 1.8, 1.9,; maximum carapace width 1.0, 1.2; eye field length 1.0, 1.1; eye row I width 0.9, 1.1. Eyes aligned along their dorsal rims, ALE's diameter ½ of AME, clypeus very low, bare, chelicerae short. First eye row surrounded by thin and very sparse colorless setae; with no contrasting marks. Three stout curved median bristles below AME: two near clypeus edge and one slightly above. Abdomen grey. *Legs:* Leg formula 4-1-3-2; patella-tibia I length 1.5, 1.9; patella-tibia III length shorter than IV. Legs I brown, legs II-IV light brownish-grey. Femur I fawn, ventro-retrolateral edge with a dense row of short, stout black setae opposing corresponding row of setae on tibia. Tibia I compressed but ex-

panded dorso-ventrally and rounded, making an oval plate, with dorsal surface slightly flat and with distinct dorso-lateral edges, lateral surfaces dark brown, dorsal and ventral surfaces lighter. Tibia I width 41% of its length; six pairs of ventral spines; a thin crest of dense flattened setae, dark and long, on prolateral side of femur. Metatarsus I thin and long, with short but robust ventral spines (four prolateral and three retrolateral). *Palp:* Typically euophryine, with meandering seminal receptacle canal and thin, anterior embolus, twisted into a coil, in this species making only half a circle (Figs. 45, 46). Cymbium twice as long as the bulb, and slightly longer than tibia; tibial apophysis slim and short, straight in ventral view, but laterally appears half-crescent shaped.

Female: (n = 5). Total length 4.6–5.0 ($\bar{x}$ = 4.72), length of carapace 1.8–2.0 ($\bar{x}$ = 1.88), maximum carapace width 1.0–1.2 ($\bar{x}$ = 1.12), eye field length 1.0–1.2 ($\bar{x}$ = 1.10), eye row I width 1.0 ($\bar{x}$ = 1.00). Ventral aspect generally pale, whitish-yellow. *Legs:* Leg formula 4-1-3-2; patella-tibia I length 1.5–1.6 ($\bar{x}$ = 1.56), patella-tibia III length shorter than IV. Leg I pale yellow, with some greyish darkening. Abdomen light-grey divided by white line, accented by a white transverse line in the dorsal depression, on sides turning diagonally. Tibia I cylindrical, with flattened dorsal surface, six pairs of ventral spines but no ventral crest of setae. Width of femur I 36% of its length, tibia I 16%. Femur I without row of strong setae along retro-lateral edge, but some indistinct and sparse setae along that edge. *Epigynum:* consists of a pair of large but indistinct openings located on the background of translucent spermathecae; internal structures consist of two sclerotized chambers followed by a heavily sclerotized, short convoluted duct, leading into a spherical spermathecae. Pores are in two separate parts, also found in other Euophryinae: a distinct funnel-like structure near fertilization canal at the spermathecae producing a tight group of hair-like structures reaching center of spermathecae; also a porous structure (without actual opening visible) in wall of sclerotized entrance chamber.

Material examined.—**FIJI**: *Viti Levu,* Lomaivuna district, about 3 km N of Nanggali, tree shaking in pine, 1♂2♀, 30 May 1987 (JWB & ERB). Lami (near Suva), tree in field, 1♂(holotype)1♀1imm, 23 May 1987 (JWB & ERB). Nausori Highlands, 500–700 m, 1♂, November 1976 (N.L.H. Krauss) (BPBM). Mbau District at C.A.T.D. campus stream, near Mbau Landing, 3♀, 31 May 1987 (JWB & ERB). Hill forest 8 miles NE of Navua, tree shaking, 1♀, 2 May 1987 (JWB & ERB). Nanduri Village, shaking shrubs on hill side; elev. 100 ft., 1♀, 21 May 1987 (JWB & ERB). *Ovalau,* Levuka, 1♂, December 1969 (N.L.H. Krauss) (BPBM).

Distribution.—Known only from the islands of Viti Levu and Ovalau in Fiji.

Genus *Ergane* L. Koch 1881

Discussion.—This genus currently includes three species (Prószyński 1990): *E. cognata* L. Koch 1881, known only from the type specimen from the Pellew Islands, Australia (Davies & Żabka 1989), *E. insularis* L. Koch 1881, from Pellew Islands (type missing from the Hamburg Museum which has the types of Koch's other *Ergane* species (Rack 1961)), and *E. benjarei* (Peckham & Peckham 1907), from Sarawak, Borneo, type location unknown to us. These species are all said to have the ocular quadrangle wider behind than in front (Davies & Żabka 1989; Peckham & Peckham 1907; Simon 1901–03). The new species described here has the ocular quadrangle narrower behind. It otherwise closely resembles figures of *E. cognata* in Davies & Żabka (1989).

Diagnosis.—A large fissidentate salticid with lateral spines on metatarsus I, anterior coxae separated by more than a coxal diameter, retromarginal cheliceral tooth tricuspid, promarginal tooth bicuspid.

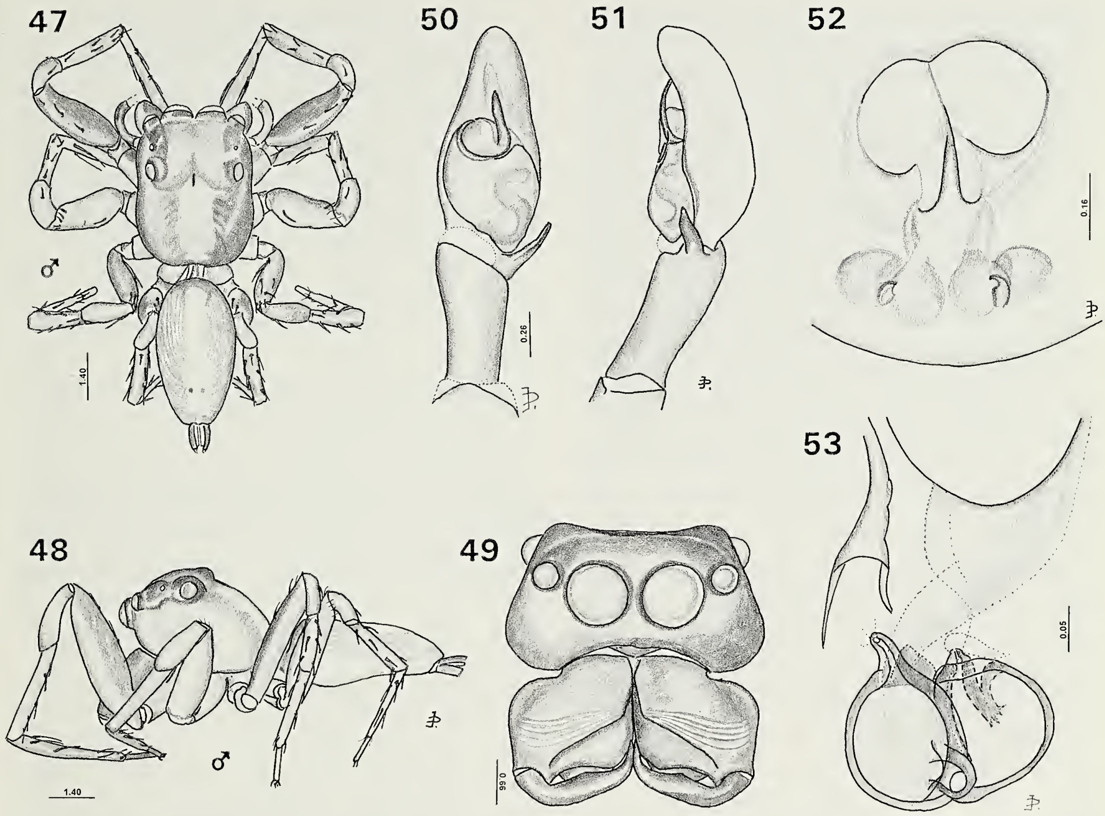
Ergane carinata new species
Figs.47–53

Holotype.—Male from Caroline Islands, Palau, Arakabesan Island, 23 March 1973 (JAB & JWB) (BPBM).

Etymology.—The name, *carinata,* refers to the distinctive ridges on the anterior face of the male chelicerae.

Diagnosis.—Male palp typically euophryine with relatively broad embolus, chelicerae broad and diverging, with diagonal ridges in their anterior apical part; female epigynum with two oval windows located far anteriorly. Retrolateral cheliceral tooth tricuspid.

Description.—*Male:* (n = 5). Total length 7.8–10.3 ($\bar{x}$ = 9.06), length of carapace 3.5–4.8 ($\bar{x}$ = 4.13), maximum carapace width 2.8–



Figures 47–53.—***Ergane carinata*** new species from Palau (Caroline Islands). 47, Dorsal appearance of male; 48, Lateral appearance of male; 49, Face of male; 50, Palpal organ ventrally; 51, Palpal organ laterally; 52, Epigynum; 53, Internal structure of epigynum showing right spermatheca and duct.

3.8 ($\bar{x}$ = 3.34), eye field length 1.8–2.2 ($\bar{x}$ = 2.02), eye row I width 2.3–2.8 ($\bar{x}$ = 2.53). Carapace dark brown, with light median streak along thorax, black lateral and anterior edges of the eye field, eyes III risen half of their diameter above eye field, dorsum of carapace gently rounded, the highest point just before eyes III, sloping posteriorly from there. Abdomen narrower than carapace, elongate and pointed posteriorly, with dorsal surface and upper sides with dense dark greyish brown lines, separated by chains of yellowish dots; there is a yellowish-white median streak, narrowed in two places; spinnerets thin and elongate, dorsally dark, ventrally light. Dorsal edges of ALE are positioned slightly above AME, their diameter about half of the AME. Chelicerae broad and diverging, anterior surfaces flattened, with several peculiar diagonal ridges in their apical part; fangs very large. One (3-cusped) retrolateral cheliceral tooth, one prolateral cheliceral tooth (2–3 cusped; 3rd cusp, when present, tiny). Fang furrow with a slight depression for reception of tooth. Chelicerae, endites and coxae I posteriorly dark chestnut brown. Lower external part of carapace appears swollen and rounded, somewhat resembling *Ascyltus pterygodes* (L. Koch 1865). Sternum and remaining coxae yellow, abdomen ventrally lighter yellow with darker, greyish median area. *Legs:* Leg formula 1-2-4-3; patella-tibia I length 3.4–5.2 ($\bar{x}$ = 4.54), patella-tibia III longer than IV. Legs not particularly robust, segments beyond coxae brownish-yellow, legs II-IV yellow to brownish-yellow, with darker femora and darker annuli on tibiae. Numerous long spines, on tibiae I-IV in two rows on lateral surfaces, which resembles *Ascyltus*. There are other short setae on the legs, particularly ventrally on leg I, but less striking than in *Ascyltus. Palp:* Pedipalps thin, their femora bent, tibia long; embolus differs from *Ascyltus* Karsch 1878 by having a broad, flattened

shape; otherwise, these organs are rather similar in shape and proportions.

Female: (n = 5). Total length 6.7–8.6 ($\bar{x}$ = 7.76), length of carapace 3.1–3.9 ($\bar{x}$ = 3.64), maximum carapace width 2.4–3.0 ($\bar{x}$ = 2.73), eye field length 1.7–1.9 ($\bar{x}$ = 1.81), eye row I width 2.0–2.4 ($\bar{x}$ = 2.25). Chelicerae differ from male by having normal proportions and shape; much lighter, yellowish coloration with darker areas in the same pattern as male. Face similar to male, but cheeks less pronounced. *Legs:* Legs much shorter than in male and uniformly yellow, but location and number of spines similar. Leg formula 4-1-3-2; patella-tibia III longer than IV. Patella-tibia I length 2.1–2.8 ($\bar{x}$ = 2.52). *Epigynum:* With two large rounded windows anteriorly, behind are a pair of bilobed spermathecae.

Material examined.—CAROLINE ISLANDS: *Palau*, Angaur, in *Triumfetta* litter, 1♀, 27 April 1973 (JAB, JWB, ERB). Angaur, mixed tropical forest, tree shaking, 1♀1imm., 30 April 1973 (JWB, ERB & JAB). Angaur, banana-betel palm forest, 5♂3♀5imm., 27 April 1973 (JWB, ERB & JAB). Arakabesan, 1♂(holotype)1♀, 23 March 1973 (JWB, JAB). Arakabesan, mixed tropical forest, 1♀, 16 March 1973 (JWB & JAB). Koror, taro patch on shrubs, 2♂2♀, 2 April 1973 (JWB & JAB). Koror, taro patch, 4♂1♀3imm., 7 March 1973 (JWB & JAB). Koror, mangrove-taro, sweeping, 1♂, 31 January 1973 (JWB & ERB). Koror, banana-almond forest, near museum bai, hand collected, 2♂1imm., 31 January 1973 (JWB & ERB). Koror, vacant lot near bai, 2♂2♀, 25 March 1973 (JWB). Koror, vacant lot, 1♂1♀2imm., 22 March 1973 (JWB). Koror, scrub forest in vacant lot, sweeping, 2♂3imm., 14 May 1973 (JWB & JAB). Koror, scrub forest in vacant lot, tree shaking, 2♂, 13 February 1973 (JWB). Koror, scrub forest in vacant lot, sweeping, 3♂4imm., 13 March 1973 (JWB & JAB). Koror, laboratory building, 1♀1imm., 26 February 1973 (JWB). Koror, on laboratory building, 1♂1♀, 8 March 1973 (JAB). Koror, laboratory building, 2♀, 6 March 1973 (JWB). Koror, cave entrance, 1♂1♀1imm., 17 March 1973 (JWB & JAB). Babelthuap, Ngaremlengui, in woods, 2♂3♀2imm., 21 April 1973 (JWB, ERB & JAB). Babelthuap, Nekkin, open eucalyptus forest, sweeping and tree shaking, 2♀1imm., 3 February 1973 (JWB & ERB). Babelthuap, Airai, below SDA school, mixed tropical forest, tree shaking, 1♂1♀1 imm., 11 March 1973 (JWB, ERB & JAB). Babelthuap, Airai, betel palm forest, 1♀1imm., 11 March 1973 (JWB, ERB & JAB).

Distribution.–Known only from Palau in the Caroline Islands.

Genus *Euophrys* C.L. Koch 1834

Discussion.—This large, primarily Holarctic genus includes also some species of sub-Saharan Africa, Central and South America and southern Asia. It is absent from Australia (Davies & Żabka 1989) and has not previously been reported from anywhere in the Pacific region except Japan and New Zealand.

We have several very small species with similar external appearance but differing in length of embolus and internal structure of the epigynum. Logunov et al. (1993) recently questioned the diagnostic value of the epigynum and its internal structure for some species.

Diagnosis.—Small, usually unidentate non-antlike salticids, lacking lateral spines on tibia I. Fourth legs longer than others, but all legs relatively short and not differing very much in length. The carapace is short and high, with the cephalic region longer than thoracic region (Fig. 54). Second row of eyes midway between first and third rows.

Descriptive notes.—The species described here are characterized by minute size, high and broad carapace, with more than half of its length occupied by the eye field, the flat surface of the carapace making up ¼ of its length, and the posterior slope of thorax very steep. Abdomen usually shorter and narrower than carapace, except in females. Anterior eyes in a straight row, aligned along their dorsal rims; ALE's diameter ⅔ of AME's, clypeus low, ⅙ of AME's diameter. Chelicerae small—equal to AME's diameter. Clypeus almost bare, with three bent bristles under junction of AME. Cheliceral dentition variable: in ***Euophrys wanyan*** new species and ***Euophrys kororensis*** new species there is a bicusp (fissidentate) retromarginal tooth. In ***Euophrys bryophila*** new species there is a single cusp retromarginal tooth, as in Palaearctic species.

Euophrys wanyan new species
Figs. 54–58, Map 4

Holotype.—Male, from Yap Island, Wanyan, dead coconut fronds, 17 April 1980 (JAB & JWB) (BPBM).

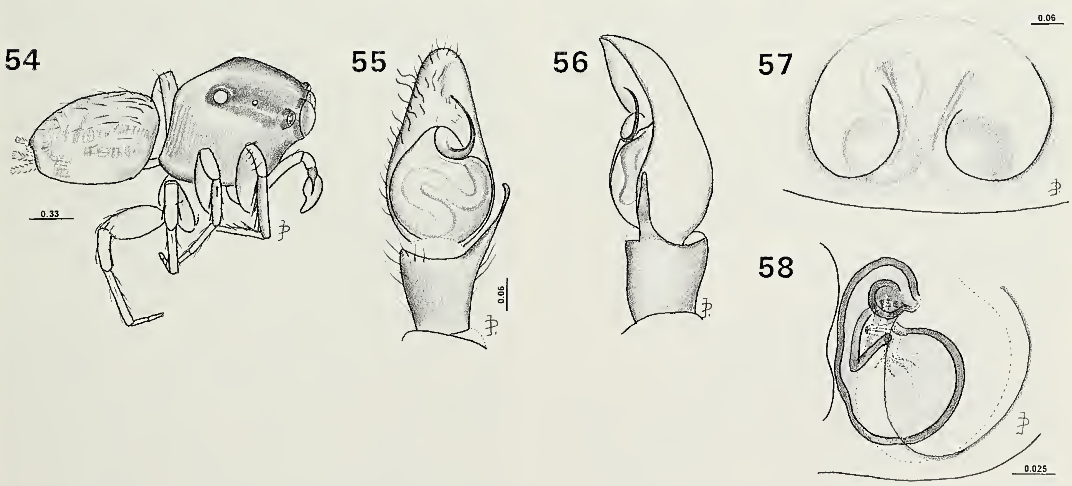
Etymology.—The name *wanyan* is a noun in apposition after the village of Wanyan, Yap, where the specimens were collected.

Diagnosis.—Embolus making half-coil, narrower than in *Euophrys kororensis*, sclerotized duct in epigynum short, its width about ⅓ of diameter of spermatheca.

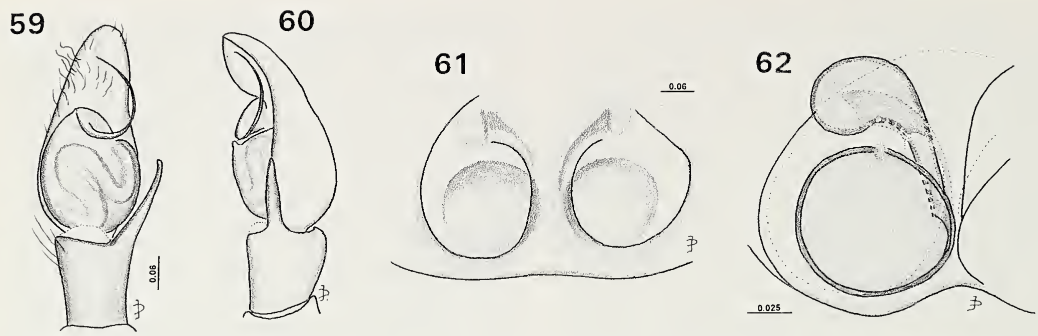
Map 4.—Distribution of ***Euophrys wanyan*** new species (★) from the Yap Islands, ***Euophrys kororensis*** new species (■) from the Palau Islands, and ***Euophrys bryophila*** new species (□) from Fiji.

Description.—*Male:* (n = 5). Total length 2.4–2.6 ($\bar{x}$ = 2.47), length of carapace 1.2–1.4 ($\bar{x}$ = 1.28), maximum carapace width 0.9–1.0 ($\bar{x}$ = 0.94), eye field length 0.8 ($\bar{x}$ = 0.80), eye row I width 0.9–1.0 ($\bar{x}$ = 0.96). Small area on anterior of thorax, narrow streak below lateral eyes and narrow streak along lower sides whitish-yellow, posterior slope of thorax and major part of middle sides brown with some vertical darker lines. A dark streak along the ventral edge; eye field dark grey, lateral edges of eye field blackish, with remnants of inconspicuous fine whitish setae above eyes I. A few sparse colorless setae around margins of eye field; otherwise, carapace almost bare. Abdomen light grey, minutely light yellowish spotted, anterior dorsal half lighter yellow suffused with grey, the posterior half with an indistinct pattern of light transverse lines; lower sides whitish, upper sides with mosaic of indistinct darker and lighter areas. Face light yellowish-brown, suffused with grey, contrasting with dark eye field; chelicerae yellowish-brown suffused grey, pedipalps yellow. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. Setae surrounding eyes I inconspicuous whitish; clypeus bare with darker edge. Ventral aspect generally light yellow and whitish; chelicerae light brownish yellow, with a fissidentate bicusp tooth on retrolateral edge. *Legs:* Leg formula 4=3-2-1, patella-tibia III length equal to IV. Patella-tibia I length 0.8 ($\bar{x}$ = 0.80). Ventral spines of tibia I: outer row, 3; inner row, 3. Metatarsus I with three pairs of long ventral spines (the basal one reaching middle of tarsus) and two pairs of shorter lateral spines, tibia I retrolaterally with five ventral spines and one lateral, prolaterally with three ventral spines and two lateral. *Palp:* Bulb broad oval, with coil of embolus anteriorly, embolus long, making a half-turn, unusual waving hairs antero-laterally on cymbium, apophysis long and thin, slightly bent apically.

Female: (n = 5). Total length 3.0–3.3 ($\bar{x}$ =



Figures 54–58.—***Euophrys wanyan*** new species, from Caroline Islands: Yap Island. 54, General appearance of male; 55, Palpal organ ventrally; 56, Palpal organ laterally; 57, Epigynum; 58, Internal structure of epigynum, showing single spermatheca and ducts.



Figures 59–62.—***Euophrys kororensis*** new species, from Caroline Islands: Palau. 59, Palpal organ ventrally; 60, Palpal organ laterally; 61, Epigynum; 62, Internal structure of epigynum --single spermatheca and ducts.

3.12), length of carapace 1.3–1.5 ($\bar{x}$ = 1.40), maximum carapace width 1.0–1.2 ($\bar{x}$ = 1.10), eye field length 0.8–0.9 ($\bar{x}$ = 0.71), eye row I width 1.0–1.1 ($\bar{x}$ = 1.08). Cheliceral teeth as in male. *Legs:* Leg formula 4-3=1-2, patella-tibia III length about equal to IV Patella-tibia I length 0.9–1.1 ($\bar{x}$ = 1.00). Ventral spines of tibia I: outer row, 5; inner row, 4. *Epigynum:* With transverse oval white membranous window, spermathecae relatively small, sclerotized copulatory duct short, membranous duct inconspicuous and short, directed back (Figs. 57, 58).

Material examined.—CAROLINE ISLAND: *Yap,* Wanyan, dead coconut fronds, 1♂(holotype)2♀, 17 April 1980 (JAB & JWB). Gilman Point, 1♂, beach litter, 1♀, coconut undergrowth, 29 May 1973 (JWB & JAB). Gilman Point, 1♂, sweeping low vegetation; 2♀, among dead coconut fronds; 2♂1♀, beach litter, 15 April 1980 (JWB & JAB). Fedor, under rocks, 1♀, 6 April 1980 (JWB & ERB). Fedor, under rocks, 1♂, 9 April 1980, (JAB & JWB). Fedor, coconut trash,1♀, 7 February 1980 (JAB & JWB). Aringel, 1♀, tree shaking, 3 March 1980 (JWB & JAB). *Map,* Chool, 1♀, on coconut trunk, 12 April 1980 (JAB & JWB).

Distribution.—Known only from Yap in the Caroline Islands.

Euophrys kororensis new species
Figs. 59–62, Map 4

Holotype.—Male from Caroline Islands, Palau, Koror Island, litter at edge of taro patch, 2 April 1973 (JWB & JAB) (BPBM).

Etymology.—The species name, *kororensis,* is after the island of Koror, Palau, where the specimens were collected.

Diagnosis.—Embolus making half-coil, broader than in *Euophrys wanyan,* sclerotized duct in epigynum short, its width about ⅛ of diameter of spermatheca.

Description.—*Male:* (n = 5). Total length 2.3–2.6 ($\bar{x}$ = 2.42), length of carapace 1.2–1.3 ($\bar{x}$ = 1.24), maximum carapace width 0.9–1.0 ($\bar{x}$ = 0.98), eye field length 0.8–0.9 ($\bar{x}$ = 0.82), eye row I width 0.9–1.1 ($\bar{x}$ = 1.02). Anterior part of thorax, narrow streak below lateral eyes and lower sides whitish-yellow, posterior slope of thorax and middle sides brown with some vertical darker lines: there is a very thin dark line along the ventral edge. Eye field dark grey with lateral edge of eye field blackish. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. Abdomen light grey dorsally, minutely light yellowish spotted in the posterior half with a few light transverse lines, one in the form of a slightly broader chevron; sides conspicuously whitish. Face light, yellow suffused, grey under AME, contrasting with dark eye field; chelicerae yellow suffused, pedipalps yellow. Ventral aspect generally light yellow and whitish. *Legs:* Leg formula 4=3-2=1, patella-tibia III length equal to IV. Patella-tibia I length 0.8–0.9 ($\bar{x}$ = 0.84). Legs yellowish-white, lateral surfaces of tibiae I-II greyish, III-IV slightly darkened with darker apical parts, femora I-IV whiter with contrasting dark greyish spots apically on lateral surfaces. Ventral spines of tibia I: outer row, 4; inner row, 4. Metatarsus I with three pairs of long ventral (the basal one reaching middle of tarsus) and two pairs of shorter lateral spines. *Palp:* Closely resembles *E. wanyan,* but bulb slightly longer and narrower, coil of embolus

broader, embolus longer, cymbium longer, with similar waving hairs, apophysis longer and slightly less bent apically (Figs. 59, 60).

Female: (n = 2). Total length 3.0, 3.1; length of carapace 1.5, 1.6; maximum carapace width 0.9, 1.1, eye field length 0.8, 0.9; eye row I width 1.1, 1.2. Carapace differs from *Euophrys wanyan* by lighter eye field, greyish-yellow between black lateral rims, narrowing light area on anterior thorax extends to rear thoracic margin, limited in the middle of slope by a pair of narrow diagonal brown streaks, extending anteriorly along middle of sides to level of eyes II. Thin dark line along the ventral edge. Face light yellow, whitish under ALE, contrasting with dark eye field; eyes I surrounded with indistinct whitish setae, clypeus more or less bald. Cheliceral teeth as in male. Chelicerae yellow, pedipalps yellow. Ventral aspect generally light yellow and whitish. Abdomen as in *Euophrys wanyan* with grey and whitish pattern consisting of crooked and straight lines, sides with mosaic of lighter and darker spots. *Legs:* Leg formula 4-3-1-2; patella-tibia I length 1.0, 1.1; patella-tibia III length equal to IV. Ventral spines of tibia I: outer row, 5; inner row, 4. Metatarsus I spines as in male. *Epigynum:* With transverse oval white membranous window, spermathecae relatively larger, sclerotized copulatory duct short, membranous duct inconspicuous and short, directed back (Figs. 61, 62).

Material examined.—CAROLINE ISLANDS: *Palau*, Koror, taro patch litter, 1♂(holotype)1♀, 2 April 1973 (JAB & JWB). Koror, taro patch litter, 1♀2imm., 26 March 1973 (JAB & JWB). Koror, #2 taro patch litter, 1♂, 3 April 1973 (JAB & JWB). Koror, banana trash below lab, 1♂, 20 February 1973 (JAB & JWB). Koror, taro patch litter, 1♂1♀1imm., 30 March 1973 (JWB & JAB).

Distribution.—Known only from Koror Island, Palau, in the Caroline Islands.

Euophrys bryophila new species
Figs. 63–69, Map 4

Holotype.—Male from Fiji, Viti Levu: Mt. Tomanivi, 1320 m, summit moss forest, moss litter, 20 August 1978 (S. & J. Peck) (AMNH).

Etymology.—The name, *bryophila*, is based on the habitat in which the specimens were collected.

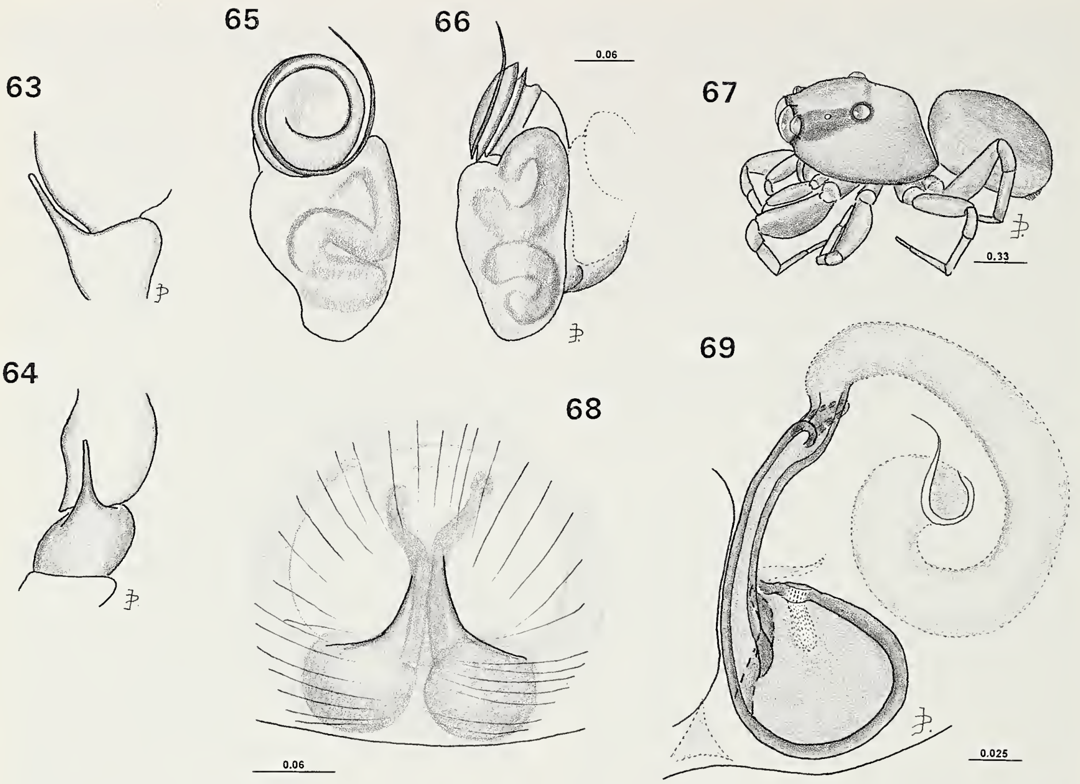
Diagnosis.—Embolus makes a full, broad circle, epigynum with sclerotized ducts unusually long, running straight anteriorly, before passing into membranous coil. Placement in this genus is uncertain.

Description.—Both sexes, stocky, tegument strongly sclerotized, brown, without contrasting pattern. Carapace broadest at eyes I.

Male: (n = 3). Total length 1.75–1.85 ($\bar{x}$ = 1.80), length of carapace 1.00–1.05 ($\bar{x}$ = 1.03); maximum carapace width 0.80–0.85 ($\bar{x}$ = 0.82), eye field length 0.60–0.65 ($\bar{x}$ = 0.62), eye row I width 0.80–0.90 ($\bar{x}$ = 0.85). Carapace almost uniformly brown, bare, shiny. Abdomen dark brownish-grey, with a few lighter spotted diagonal lines, sometimes a thin unpigmented median line. In some specimens the dorsal tegument forms a scutum; in others may be more strongly sclerotized, but does not form a distinct scutum. Face, chelicerae, and pedipalps greyish-brown, only cymbium and tips of chelicerae yellow; setae around eyes I inconspicuous; clypeus bare. Ventral aspect generally brown, abdomen greyish-brown. Chelicerae light with a single cusp tooth on retrolateral edge (unidentate). *Legs:* Leg formula 4-3=1-2, patella-tibia I length 0.55–0.65 ($\bar{x}$ = 0.60), patella-tibia III length shorter than IV. Legs I greyish-brown. Tibia I with three pairs of ventral spines only, metatarsus with two pairs of long ventral spines and one pair of short lateral spines apically; all spines more or less upright, some perpendicular. *Palp:* membranous base of bulb partially inflated, pushing bulb and embolus out of cymbium, comparison of palp with that of other species difficult; tibial apophysis straight and thin (Figs. 63–66).

Female: (n = 3). Total length 2.0–2.3 ($\bar{x}$ = 2.17), length of carapace 1.1–1.2 ($\bar{x}$ = 1.13); maximum carapace width 0.90–0.95 ($\bar{x}$ = 0.92), eye field length 0.7–0.8 ($\bar{x}$ = 0.73), eye row I width 0.9–1.0 ($\bar{x}$ = 0.92). *Legs:* Leg formula 4-3=1-2; patella-tibia I length 0.6–0.8 ($\bar{x}$ = 0.68), patella-tibia III length shorter than IV. Coloration and spination as in male. *Epigynum:* With almost round white membranous window, spermathecae small, sclerotized copulatory duct long and almost straight, extended by a broad membranous coiled duct (Figs. 68, 69).

Material examined.—Only the type collection: holotype male, plus 3♂5♀, all from Fiji, Viti Levu: Mt. Tomanivi, 1320 m, summit moss forest, moss litter, 20 August 1978 (S. & J. Peck) (AMNH).



Figures 63–69.—***Euophrys bryophila*** new species, from Fiji: Viti Levu. 63, Tibial apophysis dorsally; 64, Tibial apophysis laterally; 65, Bulb and embolus of the expanded palpal organ, ventrally; 66, Bulb and embolus of the expanded palpal organ, laterally; 67, General appearance of male; 68, Epigynum; 69, Internal structure of epigynum --single spermatheca and ducts.

Distribution.—Known only from Viti Levu, Fiji.

Genus *Evarcha* Simon 1902

Discussion.—This large genus contains some 35 species in the Old World, including nine in the Oriental Region, of which only *Evarcha hyllinella* Strand 1913 (from Polynesia and Lombok) is a geographic neighbor; but according to the drawing of its epigynum in Strand 1915, it does not seem to be related. On the other hand, *Mollica pusilla* Strand 1913 from Tahiti, shown in Strand 1915 is apparently an *Evarcha*, although a different species. Many of the Oriental species have externally similar epigyna and can be distinguished only by the internal structure of epigynum.

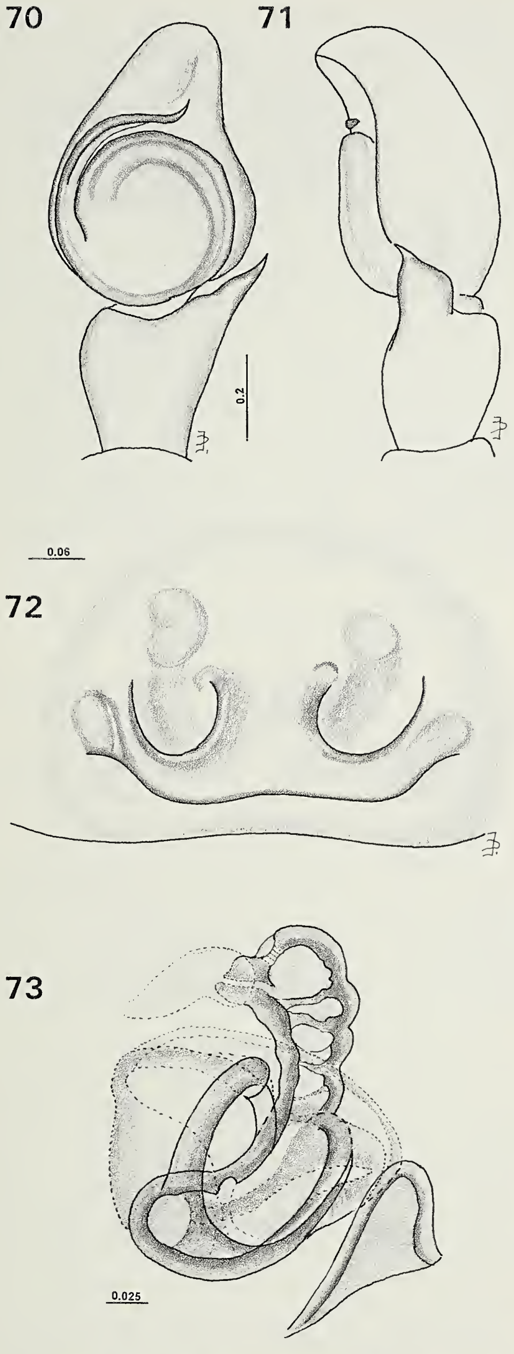
Diagnosis.—Medium-sized unidentate salticids, usually placed close to the genera *Habronattus* F.O.P.-Cambridge 1901 and *Pellenes* Simon 1876, which they resemble in external appearance. They differ by lacking the palpal conductor present in Habronattus and having a basal prolongation of the bulb, not present in other genera. The epigynum lacks the central hood found in *Habronattus* and has the openings larger and further apart than *Pellenes*.

Evarcha reiskindi new species
Figs. 70–73

Holotype.—Female from Palau Islands, Malakal, grass sweeping, elev. 100 ft., 14 March 1973 (JWB & JAB) (BPBM).

Etymology.—This species is named for Dr. Jon Reiskind, an arachnologist at the University of Florida, Gainesville.

Diagnosis.—Palpal bulb round, embolus arising probasally, encircling ¼ of bulb, tibial apophysis in lateral view broad with top cut diagonally, ventrally thin, pointed; epigynum short and broad, unusual by chambers of spermatheca extending straight anteriorly, membranous duct broad, making a single coil.



Figures 70–73.—***Evarcha reiskindi*** new species, from Palau in the Caroline Islands. 70, Palpal organ ventrally; 71, Palpal organ laterally; 72, Epigynum; 73, Internal structure of epigynum showing right spermatheca and ducts.

Differs from other *Evarcha* by its relatively simple spermatheca and ducts. The only Australian species, *Evarcha infrastriata* (Keyserling 1881), has a similar epigynum with relatively simple internal structure; but the drawing of it (Żabka 1993) is too diagrammatic to draw conclusions; the male palp of that species differs from the species described below by its much longer embolus, making a full circle around bulb. Both male and female of *E. infrastriata* have a striking, tight cluster of stout, curved bristles, below and between lateral eyes II-III, resembling horns.

Description.—*Male:* (n = 5). Total length 6.0–7.0 ($\bar{x}$ = 6.59), length of carapace 2.9–3.6 ($\bar{x}$ = 3.32); maximum carapace width 2.1–2.5 ($\bar{x}$ = 2.33), eye field length 1.5–1.7 ($\bar{x}$ = 1.57), eye row I width 1.8–2.0 ($\bar{x}$ = 1.96). Carapace chestnut-brown, including eye field, lateral eyes surrounded by black, with a lighter brown area behind eye field. Fovea small but distinct, and indistinct darker diagonal lines radiate from fovea. Slopes of thorax and sides with indistinct, short, sparse dark setae, lower sides with sparse whitish setae. Face light chestnut-brown, eye I rims black surrounded with inconspicuous whitish setae, clypeus low with sparse, very long upright whitish setae on darker bases, not making any contrasting spot. Chelicerae brown; one retrolateral cheliceral tooth, one (2-cusped) prolateral cheliceral tooth. Light with indistinct rows of linear brown spots on white background and a thin dark median line along anterior half of abdomen; anterior slope and sides whitish. Sparse longer dark setae and short fine bristles give abdomen somewhat hairy appearance. Ventral aspect generally light brown to brownish-yellow, with a darker brown median area ventrally on abdomen. One male specimen entirely pale yellow, with remnants of darker diagonal abdominal pattern. *Legs:* Leg formula 1-4-3-2, with patella-tibia III longer than IV. Patella-tibia I length 2.6–3.5 ($\bar{x}$ = 3.14). Legs chestnut-brown, I prolaterally blackish-brown with ventral surfaces of metatarsus, tibia and patella on legs I-II sparsely covered with longer grey setae, and a ridge of similar setae along ventro-prolateral edge of femora I-II; no such character in female. Ventral spines of tibia I, outer row = 3, inner row = 3. *Palp:* broad with a circular bulb and long embolus; relatively simple (Figs. 70, 71). Pedipalps yellow.

Female: (n = 5). Total length 5.7–8.5 ($\bar{x}$ = 7.06), length of carapace 3.1–3.5 ($\bar{x}$ = 3.22), maximum carapace width 2.2–2.5 ($\bar{x}$ = 2.29), eye field length 1.5–1.6 ($\bar{x}$ = 1.55), eye row I width 1.8–2.0 ($\bar{x}$ = 1.97). Cheliceral teeth and coloration as in male except carapace yellow, including eye field; diagonal broad streaks on abdomen more distinct and two broad dark lines on posterior half of abdomen, enclosing median oval white area. Face yellow; chelicerae yellow, basally bulging. Ventral aspect generally pale yellow, with a darker spot or area medially on abdomen, indistinct lines of darker spots on holotype. *Legs:* Leg formula 3-4-1-2, patella-tibia III longer than IV. Patella-tibia I length 2.1–2.4 ($\bar{x}$ = 2.30). Legs yellow, I slightly darker yellow, without darker spots or rings; no ventral fur on legs I-II. Ventral spines of tibia I as in male. *Epigynum:* With broad medium septum, sclerotized posterior rim and simple ducts and spermathecae (see Figs. 73, 74).

Material examined.—CAROLINE ISLANDS: *Palau*, Malakal, grass sweeping, elev. 100 ft., 1♀ (holotype), 14 March 1973 (JWB & JAB). Babelthuap, lowland tropical forest north of airstrip (Airai), 1♂, 28 March 1973 (JWB & JAB). Babelthuap, roadside above Forestry Hqs. at Nekkin, 1♂1♀, 4 February 1973 (JWB & ERB). Babelthuap, grass field at Forestry Hqs. at Nekkin, 2♂1imm., 3 February 1973 (JWB & ERB). Babelthuap, Airai, Forestry Stat., medium grass, sweeping, 1♂2imm., 4 February 1973 (JWB & ERB). On rock island east of Malakal, betel palm trash, 1imm., 8 March 1973 (JWB). Babelthuap, Ngaremlengui, grass field sweeping, 1♀, 21 April 1973 (JWB, ERB & JAB). Babelthuap, Ngaremlengui, in woods, 1♀2imm., 21 April 1973 (JWB, ERB & JAB). Babelthuap, Airai, mango tree in field, 1♀, 7 May 1973 (JWB, ERB & JAB).

Distribution.—Known only from Palau in the Caroline Islands.

Genus *Holoplatys* Simon 1885

Discussion.—This genus was recently revised by Żabka (1991), who recognized six species groups restricted to Australia, adjacent areas and New Zealand.

Diagnosis.—Very flat, rather narrow and elongate salticids, 2–11 mm in length, cheliceral retromargin unidentate or without teeth. Cephalic region occupying less than half the length of the carapace, with two shallow depressions between posterior eyes. First pair of legs robust. Tibiae of legs I and II usually without spines. Color pattern variable, from essentially unicolorous to patterns of chevrons, longitudinal stripes or transverse bands. Patterns more highly developed on abdomen than carapace, which is often unicolorous or with eye region darker. Resembles *Ocrisiona* Simon 1901 in general appearance and genitalia of both sexes. Differs from *Ocrisiona* by having cephalic depressions between the PLE and usually lacking tibial spines on legs I and II (Żabka 1991). There is some resemblance to *Pseudicius* Simon 1885 in body shape, especially flattening of carapace and proportions of length of legs, in shape of tibia I, and reduction of tibial spines. The main difference is the absence of a row of stridulatory spines on tubercles under the lateral eyes and the details of genital organs and the abdominal pattern.

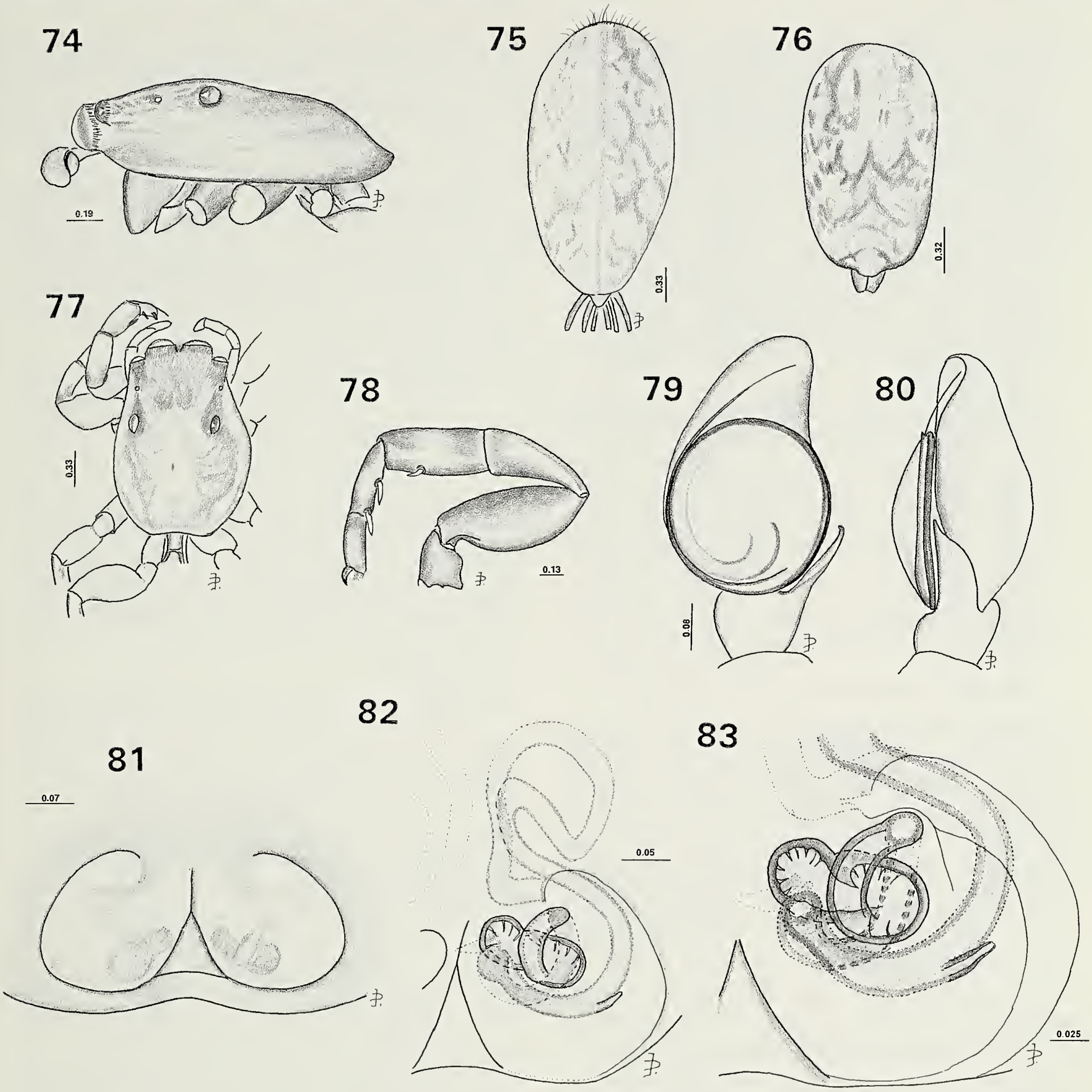
Holoplatys carolinensis new species
Figs. 74–83

Holotype.—Male from Caroline Islands, Yap, Yap Island. Fanif, on coconut trunk, 11 April 1980 (Virginia Tinnigig) (BPBM).

Etymology.—This species is named for the Caroline Islands, the only area where the species has been found.

Diagnosis.—Resembles the *H. grassalis* group (Żabka 1991) in small size, in having a tibial apophysis on the male palp and a long thin embolus. Differs from all other *Holoplatys* species, in the male, by having an almost perfectly circular tegulum and a very long thin embolus which makes about 1½ circles around the tegulum; in the female, by the relatively short broad epigynum and distinctive S-shaped course of the ducts laterally. Placement of the species in *Holoplatys* is tentative.

Description.—*Male:* (n = 2). Total length 4.2, 3.4, length of carapace 1.7, 1.7; maximum carapace width 1.1, 1.1; eye field length 0.8, 0.8; eye row I width 0.8, 0.9. Carapace low (35–36% of length), moderately broad and long, with eye field shorter than half of carapace, eyes III broader than eyes I, relatively flat surface of thorax about as long as eye field. The posterior slope of the thorax is inclined at about 45°. Colored from light-to-dark brown, with lighter spots, which make a distinct pattern, unlike the other species. Covered with setae, rather indistinct, except on sides where they are grouped into horizontal whitish streaks, separated by darker bare lines.



Figures 74–83.—***Holoplatys carolinensis*** new species. 74, Cephalothorax of male, lateral view, from Yap; 75, Abdominal pattern of female; 76, Abdominal pattern of male; 77, Cephalothorax of female, dorsal view; 78, Prolateral view of leg I of male; 79, Palpal organ ventrally, Yap; 80, Palpal organ laterally, Palau; 81, Epigynum, from Palau; 82, Internal structure of epigynum from Yap, single spermatheca and ducts; 83, Details of spermatheca and ducts of epigynum from Palau.

Alignment of eyes I approaches straight line along dorsal most part of their rim, ALE sometimes located somewhat more dorsally, diameter of ALE equal to 0.5 diameter of AME. Eye field darker than thorax, covered with more delicate and colorless adpressed setae, usually arranged angularly along the median longitudinal area; setae on the anterior part may make a whitish spot behind touching point of AME. Clypeus almost absent. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. Abdomen elongate oval, whitish grey with white internal spots visible through semi-transparent tegument; traces of darker pigmented spots with darker inconspicuous setae, in some specimens reduced to faint rudiments. *Legs:* Leg formula 1-4-2-3; patella-tibia I length 1.2, 1.2; patella-tibia III shorter than IV. Tibia I short, somewhat swollen medially. Legs spineless except for a single proventral spine each on tibiae I and IV and the pairs of ventral spines on metatarsus

I. *Palp:* Slender with slightly broader basal half of cymbium.

Female: (n = 2). Total length 4.4, 4.9; length of carapace 1.8, 1.9; maximum carapace width 1.3, 1.3; eye field I length 0.8, 0.9; eye row I width 0.9, 1.0. *Legs:* Leg formula 4-1-3-2, patella-tibia I length 1.0, 1.0; patella-tibia III shorter than IV. Females similar to males in coloration, cheliceral teeth, spination and shape. *Epigynum:* triangular median area flanked by two semicircular ridges (Figs. 81–83).

Material examined.—CAROLINE ISLANDS: *Palau*, Koror, mangrove swamp, 1♀1imm., 20 March 1973 (JWB & JAB). *Palau*, Angaur, under *Casuarina* bark, 1♂, 29 April 1973 (JWB & JAB). *Yap*, Gitam, shrub shaking, 1♀1imm., 8 April 1980 (JAB & JWB). Dalipebinau, Fanif, on coconut trunk, 1♂(holotype), 11 April 1980 (V. Tinnigig).

Distribution.—Known only from Palau and Yap in the Caroline Islands.

Genus *Myrmarachne* MacLeay 1839

Discussion.—Large genus of ant-like jumping spiders, perhaps the most widely known taxon with that type of adaptation, containing 185 species worldwide, of which as many as 108 occur in the Oriental region. Characterized by constant type of palpal organ and rather uniform type of epigynum, as illustrated in the drawings in this paper. A group of African and Asian species is often considered as genus *Belippo* Simon 1910, and the problem of separating these genera or keeping them together requires further study. Identification as the genus *Myrmarachne* begins usually by mentioning their numerous retrolateral cheliceral teeth, a character rather redundant in view of the obvious appearance. *Belippo* has a movable tibial apophysis on the male palp and secondary seminal receptacles in the epigynum (Wanless 1978a). In *Myrmarachne* the palpal tibial apophysis is immovable and the epigynum lacks secondary receptacles. Identification of species of *Myrmarachne* is difficult because of particularly uniform characters, and requires checking of all possible characters: study of stained preparation of epigyna is especially important because of complicated membranous copulatory ducts, which usually have been overlooked in studies to date. There are no publications covering all Oriental or Pacific species of this genus, and an older paper on *Myrmarachne* of the Philippines by Banks (1930) gives no details of genital organs. The fundamental revision by Wanless (1978a) is limited to Africa, but descriptions of several species were given by Żabka (1985).

Diagnosis.—The only ant-like pluridentate genus in the Pacific, distinguished also by the high cephalic region, constriction between cephalic and much lower thoracic region, slender first legs in both sexes, and greatly elongated male chelicerae.

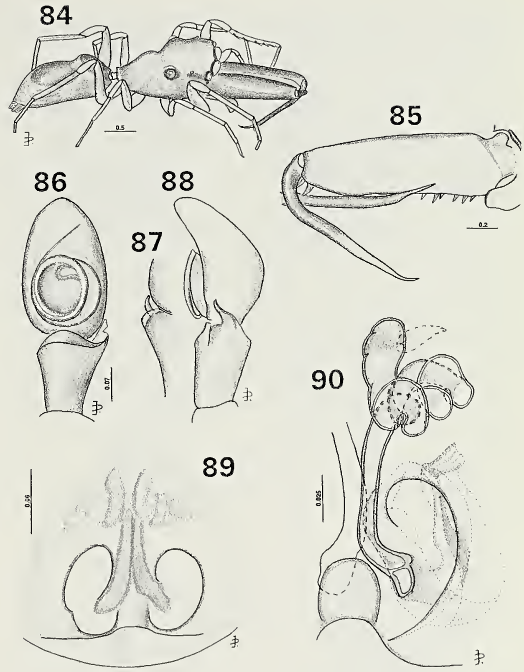
Descriptive notes.—Ant-like, color dorsally usually nearly uniform reddish-brown, sometimes lightening to yellowish. A pair of oblique lateral hair bands on abdomen ⅓–½ back. Carapace unicolorous except for black rings and bands around eyes. Legs yellowish-white with variable brown markings. Frequently a brown prolateral stripe on femur, patella and tibia. Occasionally some leg segments are entirely brown, usually femur, metatarsus or trochanter.

Carapace constricted and depressed behind eyes to varying degrees. Abdomen of males with dorsal abdominal scutum, entire or divided into anterior and posterior portions at abdominal constriction. Anterior portion of abdomen often swollen and bulging, higher than remainder of abdomen. Females lack scutum and show only a slight constriction of abdomen.

Leg spines are usually present only ventrally on first patella and first and second tibia and metatarsus. Other segments of leg I and legs III-IV lack spines. Patella I with single spine. Tibiae and metatarsi have two longitudinal rows of ventral spines. Metatarsi almost invariably have two spines in each row. Ventral tibial rows vary from 4–6 per row on tibia I and 2–4 per row on tibia II. Females tend to average one more spine per row than males on tibia I-II. Spination patterns vary little from species to species.

Genitalia in both sexes are small and rather similar among the various species. Palpal differences between species are relatively slight. Epigynum shows little detail externally with internal structure more complex, but the significance of the slight variations in coiling of the ducts is unknown at present. However, one of the authors (JP) believes that it is significant. It is likely that the more complex the coiling the more variable it is. The species

Map 5.—Distribution of ***Myrmarachne edentata*** new species (★) from the Yap Island, ***Myrmarachne pisarskii*** new species (■) from Palau and ***Myrmarachne edwardsi*** new species (□), also from Palau.



Figures 84–90.—***Myrmarachne edentata*** new species, from Yap. 84, General appearance of male; 85, Chelicera, lateral view, showing both fangs; 86, Palpal organ ventrally; 87, Tibial apophysis dorsally (shape of transparent plate uncertain); 88, Palpal organ laterally; 89, Epigynum; 90, Internal structure of epigynum, showing duct with three loops next to seminal receptacle.

may be more readily separated by non-genitalic characters.

Myrmarachne edentata new species
Figs. 84–90, Map 5

Holotype.—Male from Yap, Caroline Islands, Fedor village, Dalipebinau, shaken from trees in coconut forest, 29 January 1980 (JWB) (BPBM).

Etymology.—The name *edentata*, toothless, refers to the absence of a basal tooth on the inner margin of the fang in males.

Diagnosis.—The keeled chelicerae of the male with only the dorsal medial margin angular and the absence of a tooth on the inner margin of the fang near its base distinguish *edentata* from the other species included here. The granular eye region separates it from the other included species of which females are known. Epigynal duct forming three loops next to seminal receptacles.

Description.—*Male:* (n = 5). Total length without chelicerae 3.1–4.2 ($\bar{x}$ = 3.64), length of chelicerae 1.3–2.2 ($\bar{x}$ = 1.70), length of carapace 1.5–2.0 ($\bar{x}$ = 1.74), maximum carapace width 1.0–1.1 ($\bar{x}$ = 1.02), eye field length 0.8–0.9 ($\bar{x}$ = 0.85), eye row I width 0.9–1.1 ($\bar{x}$ = 0.96). Chelicerae with a row of 10–12 promarginal teeth, large distally and reducing to denticles proximally, and 5–6 smaller retromarginals, the two rows close together and almost merging proximally. Chelicerae somewhat longer than carapace, keeled on inner dorsal margin, sloping downward laterally, not obviously flat on top as many other species are, somewhat compressed, retrolateral teeth set on a slight ventral keel, fang slender, round in cross-section, lacking inner teeth near base, nearly straight except at base and tip. Extension of lateral surface in the form of a flap medially to fang basis, with a prominent tooth protruding anteriorly beneath the flap. Eye region of carapace and posterior lateral portions finely granular, central posterior region finely rugulose, a pair of long dorsal setae in constriction. Abdomen with complete dorsal scutum which appears divided by a constriction about ⅓ of the way back, with oblique lateral bands of white setae. *Legs:* Leg formula 4-1-2-3; patella-tibia I length 1.2–1.7 ($\bar{x}$ = 1.41), patella-tibia III longer than IV. Tibia I with 4–5 pairs of ventral spines, tibia II with 0–3 pairs, most frequently 2. *Palp:*

Tegulum smaller than in other species described here, otherwise not distinctive.

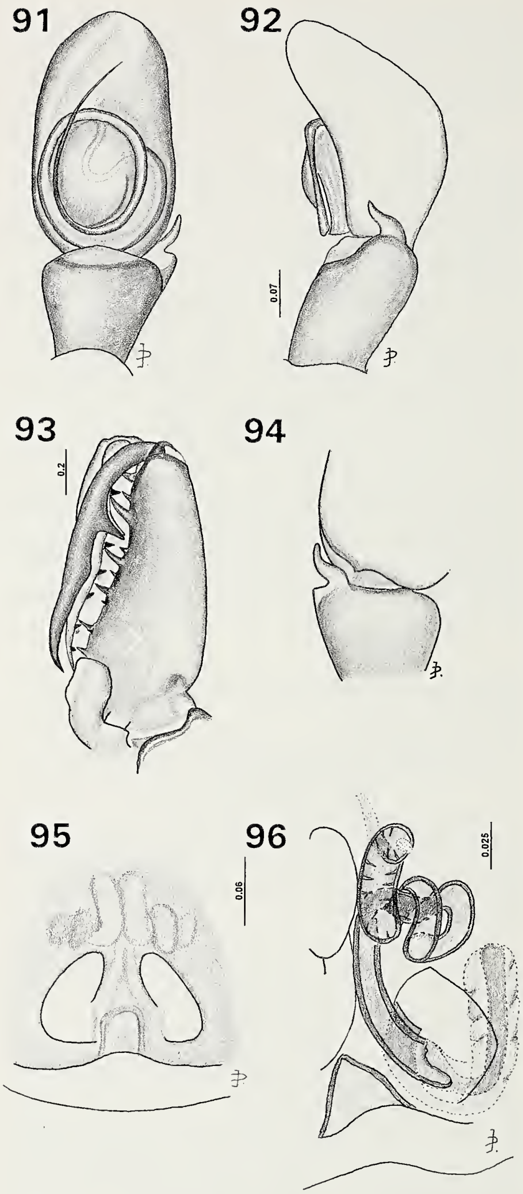
Female: (n = 5). Total length 3.5–4.6 ($\bar{x}$ = 4.02), length of carapace 1.7–2.0 ($\bar{x}$ = 1.80), maximum carapace width 0.9–1.1 ($\bar{x}$ = 1.01), eye field length 0.8–0.9 ($\bar{x}$ = 0.84), eye row I width 0.9–1.0 ($\bar{x}$ = 0.96). Chelicerae ¼ length of carapace or less, vertical; 6–7 teeth on each cheliceral margin. Carapace microsculture as in male. Overall coloration lighter brown than in male, otherwise same. Tibia I with 4–6 pairs of ventral spines (usually 5), tibia II with 1–4 pairs (usually 3). Abdomen with a lateral pair of round white spots at the level of constriction. *Legs:* Leg formula 4-1-3-2; patella-tibia I length 1.2–1.4 ($\bar{x}$ = 1.26), patella-tibia III shorter than IV. *Epigynum:* As in diagnosis (Fig. 90).

Material examined.—**CAROLINE ISLANDS:** *Yap*, Map, sweeping/shaking, 1♂2♀4imm., 30 May 1973 (JAB & JWB). Fanif, tree shaking, 2♀1imm., 11 April 1980 (JAB & JWB). Fanif, shaking dead banana leaves, 2♀1imm., 16 April 1980 (JAB & JWB). Fanif, tree shaking, 1♀1imm., 16 April 1980 (JAB & JWB). St. Mary's school, Colonia, sweeping bushes, 1♂1imm., 11 March 1980 (JWB). Colonia, burned hilltop litter, 1♂, 28 May 1973 (JWB, ERB & JAB). Colonia, tower hill, 1♀1imm., 28 May 1973 (JWB, ERB & JAB). Map, Chool, tree shaking, 1♂, 12 April 1980 (JAB & JWB). Gitam, shrub shaking, 2♀, 8 April 1980 (JAB & JWB). Fedor village, tree shaking, 1♀, 4 March 1980 (JWB). Fedor village, Dalipebinau municipality, tree shaking-coconut forest, 2♂(including holotype)2imm., 29 January 1980 (JWB). Gilman, sweeping low vegetation, 2♂, 15 April 1980 (JAB & JWB). Gilman Point, shaking bananas, 2♀, 29 May 1973 (JWB, ERB & JAB). Gagil-Tomil, shaking bananas, 2♀, 29 May 1973 (JWB, ERB & JAB). Aringel village, tree shaking, mature forest, 2♂3imm., 1 February 1980 (JWB). Ruul District, 2♂, 20 August 1950 (R.J. Goss) (BPBM). Central Yap, 1♂, 31 July 1950 (R.J. Goss) (BPBM). Yap, Caroline Is., 1♂, August 1952 (N.L.H. Krauss) (BPBM). **MARIANAS ISLANDS**: *Guam*, Mt. Lamlam, 1♀, (no date or collector) (BPBM).

Distribution.—Known only from Yap in the Caroline Islands and Guam in the Marianas Islands.

Myrmarachne pisarskii new species
Figs. 91–96, Map 5

Holotype.—Male from Caroline Islands, Palau, Babelthuap Island, Airai, shaken from tree in field, 7 May 1973 (JAB, JWB & ERB)(BPBM).



Figures 91–96.—***Myrmarachne pisarskii*** new species, from Palau. 91, Palpal organ ventrally; 92, Palpal organ laterally; 93, Chelicera, lateral view; 94, Tibial apophysis dorsally; 95, Epigynum; 96, Internal structure of epigynum showing single spermatheca and duct with two loops adjacent to seminal receptacle.

Etymology.—Named for the late Dr. Bohdan Pisarski, life-long student of ants, Professor in the Institute of Zoology, Polish Academy of Sciences and its long-time Director; a friend of one of the authors (JP) and the co-

participant in their collecting trip to Indonesia, Vietnam and North Korea in 1959.

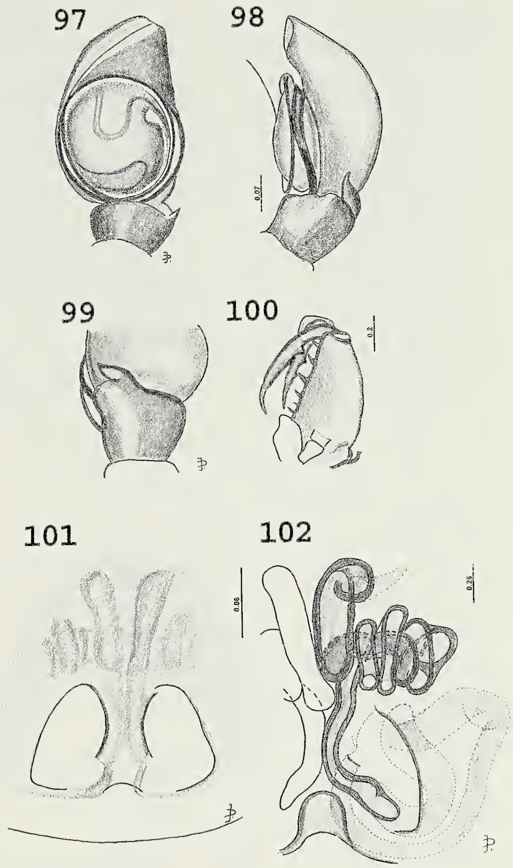
Diagnosis.—Male with a large tooth on internal margin of fang near base. Distal loop of embolus consistently narrower than proximal loop. Female epigynal duct forming only two loops adjacent to seminal receptacle.

Description.—*Male:* (n = 5). Total length without chelicerae 3.3–4.3 ($\bar{x}$ = 3.79), length of chelicerae 0.9–1.6 ($\bar{x}$ = 1.22), length of carapace 1.6–2.0 ($\bar{x}$ = 1.83), maximum carapace width 0.8–1.2 ($\bar{x}$ = 1.06), eye field length 0.8–1.0 ($\bar{x}$ = 0.88), eye row I width 0.9–1.1 ($\bar{x}$ = 0.99). Upper surface of carapace very finely granular, but also shiny, i.e., less conspicuously granular than *Myrmarachne edentata* new species. Chelicerae flattened dorsally with angular edges, almost uniform in width except dorsally; fang with large inner tooth about ⅓ length and two smaller ones just past midlength. Cheliceral teeth in two rows. Well developed post-ocular and abdominal constrictions. *Legs:* Relative leg length is 4-1-2-3; patella-tibia I length 1.2–1.9 ($\bar{x}$ = 1.50), patella-tibia III length shorter than IV. Spination as in *M. edentata.*

Female: (n = 3). Total length 4.4–5.5 ($\bar{x}$ = 4.76), length of carapace 1.9–2.4 ($\bar{x}$ = 2.10), maximum carapace width 1.1–1.4 ($\bar{x}$ = 1.20), eye field length 0.9–1.1 ($\bar{x}$ = 0.96), eye row I width 1.0–1.2 ($\bar{x}$ = 1.06). Upper surface of carapace shiny, not granular, strong post-ocular constriction. Abdomen without constriction or swelling. *Legs:* Leg formula 4-1-3-2; patella-tibia I length 1.4–1.9 ($\bar{x}$ = 1.56), patella-tibia III shorter than IV. Spination as in *M. edentata.* See descriptive notes for genus. *Epigynum:* Not externally distinguishable from other species (Figs. 95, 96).

Material examined.—CAROLINE ISLANDS: *Palau,* Babelthuap, roadside above Airai Forest Hqs., sweeping, hand collecting, 1♂3imm., 4 February 1973 (JWB & ERB). Babelthuap, Airai, tree in field, 2♂(including holotype)1♀1imm., 7 May 1973 (JAB & JWB). Babelthuap, Nekkin, mixed forest, shaking trees below forestry hqs., 1♂, 3 February 1973 (JWB & ERB). Babelthuap, Airai, tree in field, 1♂1♀, 5 May 1973. Babelthuap, Ngaremlengui, in woods, 1♂3imm., 21 April 1973 (JWB, ERB & JAB).

Distribution.—Known only from Palau in the Caroline Islands.



Figures 97–102.—***Myrmarachne edwardsi*** new species, from Palau. 97, Palpal organ ventrally; 98, Palpal organ laterally; 99, Tibial apophysis dorsolaterally; 100, Chelicera of male, lateral view; 101, Epigynum; 102, Internal structure of epigynum, showing four loops of epigynal duct adjacent to seminal receptacle.

Myrmarachne edwardsi new species
Figs. 97–102, Map 5

Holotype.—Female from Palau, Koror Island, litter adjacent to taro patch, 26 March 1973 (JAB & JWB) (BPBM).

Etymology.—Named for Dr. G.B. Edwards of the Florida State Collection of Arthropods; Gainesville, Florida.

Diagnosis.—Male with large tooth on internal margin of fang near base (Fig. 100). Distal and proximal loops of the embolus the same size, circular overlapping, usually appearing as a single loop in ventral view (Fig. 97). Female epigynal duct forming four loops adjacent to seminal receptacles.

Description.—*Male:* (n = 5). Total length

without chelicerae 3.2–4.0 ($\bar{x}$ = 3.54), length of chelicerae 0.4–1.8 ($\bar{x}$ = 1.02), length of carapace 1.4–2.1 ($\bar{x}$ = 1.72), maximum carapace width 0.9–1.2 ($\bar{x}$ = 1.03), eye field length 0.7–0.9 ($\bar{x}$ = 0.82), eye row I width 0.8–1.1 ($\bar{x}$ = 0.94). General appearance as in *Myrmarachne pisarskii.* Chelicerae flattened dorsally with angular margins. Cheliceral teeth: 5–6 small in outer row, 9 large in inner row. Eye region of carapace granular (appears minutely rugulose in one specimen from Sonsorol). *Legs:* Leg formula 4-1-3-2, patella-tibia I length 0.9–1.8 ($\bar{x}$ = 1.36), patella-tibia III shorter than IV. Ventral spines of tibia I 4–5 pairs. *Palp:* Loops of embolus forming two closely overlapping circles so that only a single loop is easily seen.

The single male from Sonsorol Island differs in sculpture of the carapace, but it is apparently recently molted and appearance might change with age. With only one specimen available, we choose not to regard it as a separate species. Likewise, we exclude it from the paratype series.

Female: (n = 5). Total length 3.2–4.9 ($\bar{x}$ = 4.15), length of carapace 1.5–2.0 ($\bar{x}$ = 1.77), maximum carapace width 0.9–1.1 ($\bar{x}$ = 1.05), eye field length 0.7–1.0 ($\bar{x}$ = 0.83), eye row I width 0.8–1.1 ($\bar{x}$ = 0.95). General appearance as in *M. pisarskii.* Chelicerae short, vertical. Eye region shiny, appearing smooth at low magnification, very minutely sculptured at high magnification. *Legs:* Leg formula 4-1-3-2; patella-tibia I length 0.9–1.6 ($\bar{x}$ = 1.22), patella-tibia III shorter than IV. Ventral spines of tibia I 4–5 pairs. *Epigynum:* Internal duct making four loops adjacent to receptacle (Fig. 102).

Material examined.—**CAROLINE ISLANDS**: *Palau,* Kayangel, sweeping in field, 1♀, 21 May 1973 (JWB). Koror, shaking banana trees, 1♀, 31 March 1973 (JAB & JWB). Koror, litter adjacent to taro patch, 1♀ (holotype), 26 March 1973 (JAB & JWB). Koror, taro patch litter, 1♂, 2 April 1973 (JAB & JWB). Malakal, grass sweeping, elev. 100 ft., 1♂, 14 March 1973 (JAB & JWB). Pulo Anna, coconut/scrub tree shaking, 2♀3imm., 7 April 1973 (JWB & ERB). Sonsorol Island, grass sweeping, 1♂, 10 April 1973 (JWB & ERB). Peleliu, mixed tropical forest, 2♂, 22 March 1973 (JWB & ERB). Ngurukdabel I., Ngaremediu, 2♂, 14 May 1957 (C.W. Sabrosky) (BPBM). S Auluptagel, 1♂, 13 December 1952 (J.L. Gressitt) (BPBM).

Distribution.—Known only from the Palau group of the Caroline Islands.

Genus *Omoedus* Thorell 1881

Discussion.—A genus of three previously described small spiders (*Omoedus kulczynskii* Prószyński 1971; *O. niger* Thorell 1881; and *O. piceus* Simon 1902) known from Indonesia, New Guinea and northern Australia. In the absence of male specimens the species described here is only tentatively placed in this genus.

Diagnosis.—Small unidentate salticid. Eye region higher than thoracic, abdomen heart shaped. Ocular quadrangle rectangular, as wide behind as in front, occupying about half the length of caphalothorax or a little less. Carapace heavily sclerotized. Male palp of the euophryine type.

Omoedus cordatus new species
Figs. 103–105

Holotype.—Female from Fiji, Vitu Levu, Nandarivatu, hill behind village, in litter, 12 April 1987 (JWB) (BPBM).

Etymology.—The name, *cordatus,* is in reference to the distinctly heart-shaped abdomen.

Diagnosis.—Long coiled membranous copulatory duct of the spherical spermathecae and two accessory gland openings (Fig. 105) differentiates this species from others of the genus. The male is unknown.

Description.—*Female:* Total length 2.6 (n = 1); maximum carapace length 1.2; maximum carapace width 1.1; length of eye field 0.6; width of first eye row 2.0; length of first tibia-patella 0.8. Carapace with integument strongly sclerotized but without warts or papillae, uniformly dark brown with sparse, indistinct, small setae; there are also minute, shiny scales, also very sparse. Entire dorsal surface of carapace is flat, inclined anteriorly, with posterior edge the highest; however, eye field is slightly higher than thorax. Posterior and lateral walls of carapace are almost vertical, carapace slightly broader behind eye field, the posterior edge of thorax rounded. Abdomen higher and broader than carapace, heart shaped, brown with indistinct rows of lighter spots, with dense brush of short but thick, curved setae along antero-dorsal edge, which is curved to accommodate the rounded thoracic edge. Frontal aspect brown, with

Figures 103–105.—***Omoedus cordatus*** new species, from Fiji, Viti Levu. 103, General appearance of female; 104, Epigynum; 105, Internal structure of epigynum, left side.

sparse inconspicuous setae around eyes I, clypeus low, appearing bare with few inconspicuous brown bristles, set diagonally above ventral edge, three curved bristles below AME. Chelicerae short, slender, brown with light tips. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. Pedipalps and femur-tibia I brown with light tips; metatarsus and tarsus I light. *Legs:* A row of stiff black setae along ventral edge of apical half of femur, making a sort of cutting edge with surfaces of patella and tibia. Legs short and slender, femora I-IV brown, patellae II-IV with dorsal surface yellow, tibiae I-III brown with light apical tips, tibia IV yellow, metatarsi and tarsi I-IV yellowish white. Leg formula 4-1-2 (3rd legs missing). Ventral spines of tibia I: outer row, 3; inner row, 3. Spines on tibia I very long, those on metatarsus I extremely long, almost touching tarsal claw. *Epigynum:* with two large membranous windows, anteriorly not separated and with complicated circular furrows on surface; simple spherical spermatheca with anterior straight, not sclerotized, copulatory duct (Figs. 104, 105).

Map 6.—Distribution of ***Palpelius namosi*** new species from Fiji (★), and ***Palpelius trigyrus*** new species (■) from Yap in the Caroline Islands.

Material examined.—Only the holotype.

Distribution.—Known only from Viti Levu in Fiji.

Genus *Palpelius* Simon 1903

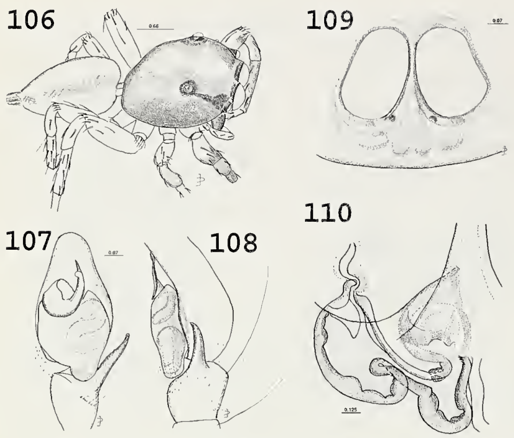
Discussion.—The genus contains nine species described from Borneo to Australia, including Mollucas and Bismarck Archipelago. No species of *Palpelius* has been described yet from Polynesia.

Diagnosis.—Unidentate salticids having leg III equal to or exceeding leg IV in length, and ocular quadrangle occupying about half the length of carapace, narrowing posteriorly. The male palp is euophryine with embolus confined to distal portion of the bulb, curving counter-clockwise (left palp). The epigynum has two large membranous windows with the copulatory openings at their posterior edges, relatively short median ducts turn outward to lateral spermathecae.

Palpelius namosi new species
Figs. 106–110, Map 6

Holotype—Female from Fiji, Viti Levu, Namosi District, hill forest on Namosi Road, about 7 km N of Queen's Road, 19 May 1987 (JWB & ERB) (BPBM).

Etymology.—Named for a region in Fiji, the Namosi District, one of the locations where this species is found.

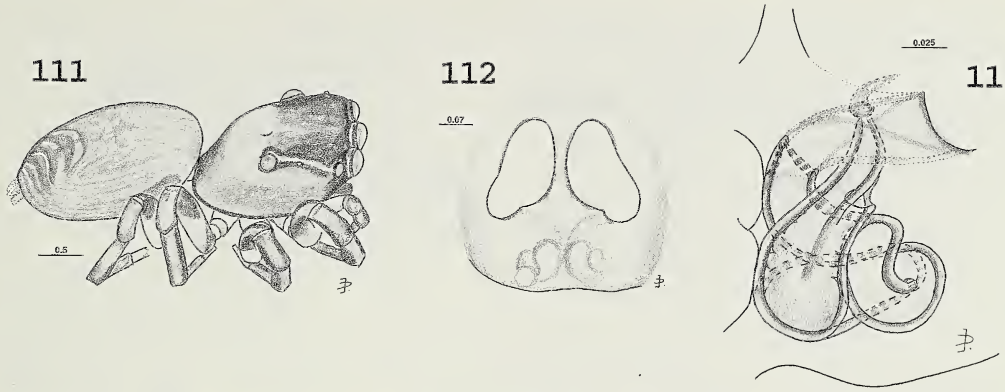


Figures 106–110.—***Palpelius namosi*** new species, from Fiji: Viti Levu. 106, General appearance of male; 107, Palpal organ ventrally; 108, Palpal organ laterally [dotted lines denote white/colorless setae]; 109, Epigynum of female from Namosi District, Viti Levu; 110, Internal structure of same epigynum showing single spermatheca and ducts.

Diagnosis.—Male with embolus broad, a flat coil on distal part of bulb, tibial apophysis long and pointed. Female with epigynal windows larger, and epigynal ducts less coiled, than in ***P. trigyrus*** new species.

Description.—*Male:* (n = 5). Total length 4.0–5.6 ($\bar{x}$ = 4.66), length of carapace 2.1–2.6 ($\bar{x}$ = 2.30), maximum carapace width 1.4–2.0 ($\bar{x}$ = 1.68), eye field length 1.0–1.5 ($\bar{x}$ = 1.22), eye row I width 1.5–1.9 ($\bar{x}$ = 1.64). Carapace sloping anteriorly, highest at level of eyes III, more gently inclined posteriorly, passing abruptly into steep posterior slope; brown, covered with adpressed, reddish, thin setae, a whitish diamond-shaped area behind eye field, covered with inconspicuous whitish setae, much thinner than the reddish ones. Abdomen elongate, narrowing posteriorly, narrower than carapace; greyish-yellow with marginal areas covered with darker grey spots making an irregular pattern and entering median streak as indistinct wedges. Sides lighter yellow with darker, grey spots, merging with light, ventral surface without spots. Spinnerets cylindrical, yellowish-grey. Frontal aspect yellowish-brown, lighter beneath eyes, eyes surrounded with red setae, clypeus low, almost bare with a few stronger bristles and sparse brown setae along edge; chelicerae narrow and short, apically rectangular with depressed transverse area and a small, flat, triangular protuberance pointed along cheliceral axis, medio-distally. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. Pedipalps whitish-yellow, with cymbium slightly darker, whitish-fawn. Several dark bristles scattered over dorsal surfaces of pedipalpal patella, tibia and cymbium, a particularly long one at the apical edge of patella and tibia, these segments and cymbium covered with grey and colorless setae. Mouth parts light brown, retrolateral tooth triangular and gently sloping; sternum, coxae and femora ventrally whitish with grey-yellow shade, abdomen whitish-grey with anterior part slightly yellowish-grey. *Legs:* Leg formula 3=4-1-2 or 3=4-2-1; patella-tibia I length 1.4–2.4 ($\bar{x}$ = 1.68), patella-tibia III equal to IV. Legs light yellowish-grey with darker, sparse short setae and numerous prominent brown spines. Ventral spines of tibia I: outer row, 3; inner row, 3 (2–3). Indistinct darkening on apical part of tibia I, femora I-IV whitish ventrally. *Palp:* Euophryine type with bulb narrow, elongate, narrowing posteriorly, embolus making flat coil on anterior ventral surface of bulb, tip of embolus appearing double due to internal duct, cymbium narrow. Palpal tibia narrow, slightly shorter than cymbium; tibial apophysis long, slightly curved; there are characteristic long bristles dorsally on tibia and patella and a few shorter ones on cymbium.

Female: (n = 2). Total length 5.4, 8.4, length of carapace 2.2, 3.4; maximum carapace width 2.0, 2.5; eye field length 1.4, 1.8; eye row I width 1.8, 2.3. Coloration as in male. Eye field chestnut-brown, almost bare but with triangle of white setae between AME; sides yellow crossed by three diagonal dark brown streaks, radiating from fovea towards coxae II-IV; a horizontal faint brown line along eye field, separating lighter yellow line below eyes III; margin of carapace brown. Face dark yellow, eyes I surrounded by reddish setae except ventrally and between AME, where white. Clypeus low, almost bare, with a few inconspicuous white setae and three curved brown bristles. Chelicerae slightly bulging, dark yellow, laterally light brownish. Cheliceral teeth as in male. Pedipalps light brown. *Legs:* Leg formula 3=4-1-2; patella-tibia I length 1.7, 2.4 with patella-tibia III about equal to IV. Legs brown with middle parts of segments slightly lighter, spines as in male. *Epigynum:* With two large anterior oval



Figures 111–113.—***Palpelius trigyrus*** new species, from Yap, Caroline Islands. 111, General appearance of female; 112, Epigynum; 113, Internal structure of epigynum showing single spermatheca and ducts.

membranous windows with copulatory openings at posterior edge of windows, broad median ducts leading to a sclerotized posterior chamber, from where a short diagonal duct leads to oval spermathecae, located laterally; entrance duct membranous (according to Davies & Żabka in *P. beccarii*, that part does not differ from spermatheca) and has a somewhat complicated structure not yet fully understood. Apparently a first accessory gland leads from entrance duct towards tegument surface; a second, porous accessory gland located near end of spermatheca.

Material examined.—**FIJI**: *Viti Levu*, Namosi District, hill forest on Namosi Road, about 7 km N of Queen's Road, 1♀(holotype), 19 May 1987 (JWB & ERB). Nandarivatu, in house, elev. 900 m, 1♂, 11 April 1987 (JWB, ERB & JAB). Nandarivatu, tree shaking, elev. 900 m, 1♀, 11 April 1987 (JWB & ERB). Nandarivatu, on abandoned building, elev. 900 m, 1♂, 11 April 1987 (JWB, ERB & JAB). Nandala Creek, 2 mi. S of Nandarivatu, sweeping/shaking. 1♂, 12 April 1987 (JWB & ERB). Nandarivatu, hill behind village, litter, 1♂, 12 May 1987 (JWB). Tholo-I-Suva Forest Park, Waisila Falls Trail, sweeping, 1♂, 11 May 1987 (JWB).

Distribution.—Known only from Viti Levu in Fiji.

Palpelius trigyrus new species
Figs. 111–113, Map 6

Holotype.—Female from Caroline Islands, Yap, Fanif, on coconut trunks, 11 April 1980 (V. Tinnigig) (BPBM).

Etymology.—The name *trigyrus* refers to the three loops of the copulatory duct.

Discussion.—Placement of this species with respect to the previous species is uncertain. However, similarity in external appearance of the epigynum, possible relation in internal structure, similar shape of carapace, similarity in proportions of length of eye field, height of carapace, length of flat surface of carapace, and similar spination of tibia I and II, suggest that they may be related. Characters suggesting different status are width of eye fields I and III and length of leg III and fissidentate cheliceral tooth. Further studies, including collecting male specimens, will be required to assign this species properly.

Diagnosis.—Membranous windows of epigynum set slightly diagonally, narrower posteriorly than in ***Palpelius namosi*** new species; copulatory duct long, making three loops (Fig. 113). The male is unknown.

Description.—*Female:* (n = 1). Total length 4.9; length of carapace 2.3; maximum carapace width 1.6; eye field I length 1.3; eye row I width 1.3. With broad, medium height carapace with expanded flattened area, broad oval abdomen. Carapace dark brown with lighter brown flat anterior part of thorax and an almost black eye field; all with sparse whitish and colorless setae. Abdomen dark grey with yellow spots along bottom of folds, making indistinct pattern (Fig. 111). Anterior eyes surrounded with orange setae and a few white ventrally; aligned straight along dorsal-most points of their rim, the diameter of ALE about 62% of that of AME. Clypeus brown, very low, almost bare, with a row of long white setae overhanging cheliceral bases. Chelicerae

of medium size, chestnut-brown, with transverse grooves. One retrolateral cheliceral tooth (bicusp), two prolateral cheliceral teeth. Pedipalps and mouth parts brown, sternum light brown, coxae yellowish; abdomen anteriorly yellowish, grey behind epigastric furrow with four lines of spots. *Legs:* Patella-tibia I length 1.5; relative length 4-1-3-2, patella-tibia III shorter than IV. Legs short and robust; dark brown, locally lighter, with ventral surface of femora whitish-yellow. Ventral spines of tibia I: outer row, 3; inner row, 3. *Epigynum:* with two white elongate oval windows separated by a thin septum, converging copulatory canals and convoluted spermathecae (Figs. 112, 113).

Material examined.—The holotype and an additional female with the same collection data.

Distribution.—Known only from Yap in the Caroline Islands.

Genus *Phintella* Bösenberg & Strand 1906

Discussion.—*Phintella* is in many ways similar to *Chrysilla* Thorell 1897, both with relatively long abdomen pointed behind, long legs and palp of non-euophryine type. Several species have been transferred from *Chrysilla* to *Phintella* recently (Platnick 1989).

Diagnosis.—Cephalothorax broad with almost parallel sides, moderately high, eyes III at the edge of flat surface. Abdomen lower and narrower than cephalothorax, gradually tapering and pointed posteriorly. Cheliceral retromarginal tooth single. Legs long and robust; with tibia I somewhat swollen and narrowing at both ends; three pairs of ventral spines and one prolateral spine, in females these spines are much reduced in length but robust; metatarsus with two pairs of ventral spines. In males leg formula is 1-4-2=3, in females 4-1-2=3.

Phintella versicolor (C.L. Koch 1846)
Map 7

Plexippus versicolor C.L. Koch 1846.
Phintella versicolor (C.L. Koch): Prószyński 1983.

Discussion.—Although it is not included in the catalog of Hawaiian spiders (Suman 1964) this species is fairly common in Hawaii. Many specimens are in the collections of the Bishop Museum and the American Museum of Natural History. A list of additional synonyms is given by Prószyński (1990).

Map 7.—Distribution of *Phintella versicolor* (★) and ***Phintella planiceps*** new species (■) from the Caroline Islands.

Material examined.—**HAWAIIAN ISLANDS**: *Hawaii County.* Kohala District, rt. 250 at Kapaau road, shaking trees, 2♂9♀1imm., 15 February 1995 (JWB & ERB); Lapahoehoe, elev. 500 ft, shaking banana leaves, 1♀, 20 February 1995 (JWB & ERB); Kolekole Park near Hilo, tree shaking, 2♂2♀6imm., 21 February 1995 (JWB & ERB); Stainback Hwy., elev. 1000 ft., shaking bushes by road, 1♂, 23 February 1995 (JWB & ERB); Opihikoa Road near Pahoa, shaking roadside bushes, 1♂1imm., 24 February 1995 (JWB & ERB).

Distribution.—Found in China, Korea, Taiwan, Japan, Sumatra and Hawaii.

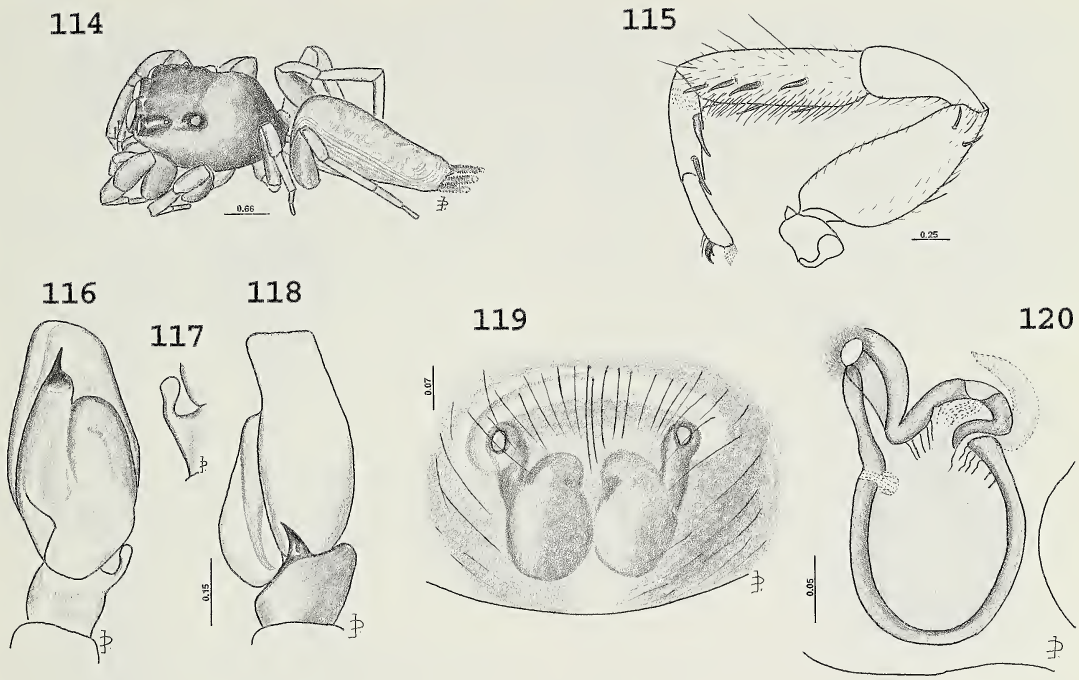
Phintella planiceps new species
Figs. 114–120, Map 7

Holotype.—Male from Ponape, palm forest E of Kolonia, 200 ft. elev., 5 June 1973 (JWB & JAB) (BPBM).

Etymology.—The name *planiceps* refers to the plane flat surface of the cephalothorax.

Diagnosis.—Distinguishable from other members of the genus by the structure of the genitalia (Figs. 116–120). Male palpal bulb deeply indented proximally near base narrowing abruptly to a short thorn-like embolus. Epigynum with ducts much shorter than in other species.

Description.—*Male:* (n = 2). Total length 5.6; carapace length 2.4; maximum carapace width 1.8; length of eyefield 1.3, 1.4; eye row I width 1.6, 1.7. Carapace brown, lightest anteriorly, eye field darker brown, thorax with indistinct lines radiating from small fovea; covered sparsely with small brown setae with



Figures 114–120.—***Phintella planiceps*** new species, from Ponape, Caroline Islands. 114, General appearance of female; 115, Leg I prolaterally of male; 116, Palpal organ ventrally; 117, Tibial apophysis dorsally; 118, Palpal organ laterally; 119, Epigynum; 120, Internal structure of epigynum, showing single spermatheca and ducts.

sparse admixture of smaller whitish setae, not making any pattern; eye field with minute, sparse, adpressed and colorless setae, and a row of longer colorless setae above eyes I. An indistinct pattern of a few pairs of small yellow spots, one larger located marginally along abdomen; small colorless and brown upright setae and larger upright sparse bristles. Face low, indistinctly higher than diameter of AME, eyes I aligned in a straight line along their dorsal rims, diameter of ALE = half that of AME, clypeus obsolete, chelicerae indistinctly longer than diameter of AME. Face and chelicerae dark brown, eyes I surrounded by inconspicuous orange setae, cymbium apically lighter with whitish setae. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. Ventral aspect of mouth parts, sternum and coxa I brown, coxae II-IV yellow. Abdomen yellowish-grey ventrally with two indistinct darker longitudinal streaks and two lines of small spots along the middle. *Legs:* Leg formula 1-4-2=3; tibia-patella I length 2.2, 2.4, patella-tibia III being shorter than IV. Leg I chestnut-brown, with patella, apical half of metatarsus and tarsus yellow; legs II-IV lighter, yellowish-fawn. Ventral spines of tibia I: outer row, 3-4; inner row, 3. Sparse ventral greyish setae on tibia I and a row of greyish setae along ventro-retrolateral edge of femur I. *Palp:* see diagnosis and Figs. 116–118. *Female:* (n = 5). Total length 5.0–6.8 ($\bar{x}$ = 5.62), length of carapace 2.3–2.8 ($\bar{x}$ = 2.44), maximum carapace width 1.7–2.2 ($\bar{x}$ = 1.86), eye field length 1.2–1.6 ($\bar{x}$ = 1.36), eye row I width 1.5–1.9 ($\bar{x}$ = 1.64). Coloration and cheliceral teeth as in male. *Legs:* Leg formula 4-1-2≥3; patella-tibia I length 1.6–2.1 ($\bar{x}$ = 1.72), with patella-tibia III shorter than IV. Ventral spines on tibia I as in male. *Epigynum:* An anterior depression is only external sculpture; oval large spermathecae and short sclerotized duct visible through tegument; opening antero-laterally, no membranous duct, pores in wall of spermatheca near junction with duct, additional pores above distal opening to the fertilization duct (Figs. 119, 120).

Material examined.—CAROLINE ISLANDS: *Ponape,* SW Sekere School, bushes on bank,

3♀1imm., 16 June 1973 (JWB & JAB). *Ponape*, E of Kolonia, palm forest, 200 ft., 1♂(holotype)1imm., 5 June 1973 (JWB & JAB). *Ponape*, Sokehs, shaking banana/breadfruit, 1♂11imm., 9 June 1973 (JWB & JAB). *Truk*, Moen Island, mixed forest above quarry, shaken from bananas, 2♀1imm., 12 June 1973 (JWB & JAB).

Distribution.—Known only from Ponape and Truk in the Caroline Islands.

Genus *Zenodorus* Peckham & Peckham 1885

Discussion.—The genus contains 16 species known from Australia, New Guinea and Pacific Islands, half of them not recognizable from existing descriptions. The type species is *Zenodorus urvillei* (Walckenaer 1837) known from New Guinea, Australia, Aru and Ceram Islands; its taxonomic characters illustrated recently by Prószyński 1984: 151 and Davies & Żabka 1989: 230, 232, pl. 35 (as *Z. durvillei*. See Bonnet 1959 for discussion of the multiple spellings of this name). The genus *Mollika* Peckham & Peckham 1901 was synonymized with *Zenodorus* by Żabka (1988).

Diagnosis.—Small to medium unidentate salticids with cymbium of male palp 1.5–2.0 times length of bulb, and embolus forming a small tight coil at distal end of bulb (Figs. 124, 125). Female with epigynal openings lying in oval areas separated by a septum. Ducts of epigynum forming three-to-many loops which lie posterior to septum (Figs. 127, 129). With a characteristic black and white pattern (Figs. 122, 123). See also figures in Davies & Żabka (1989).

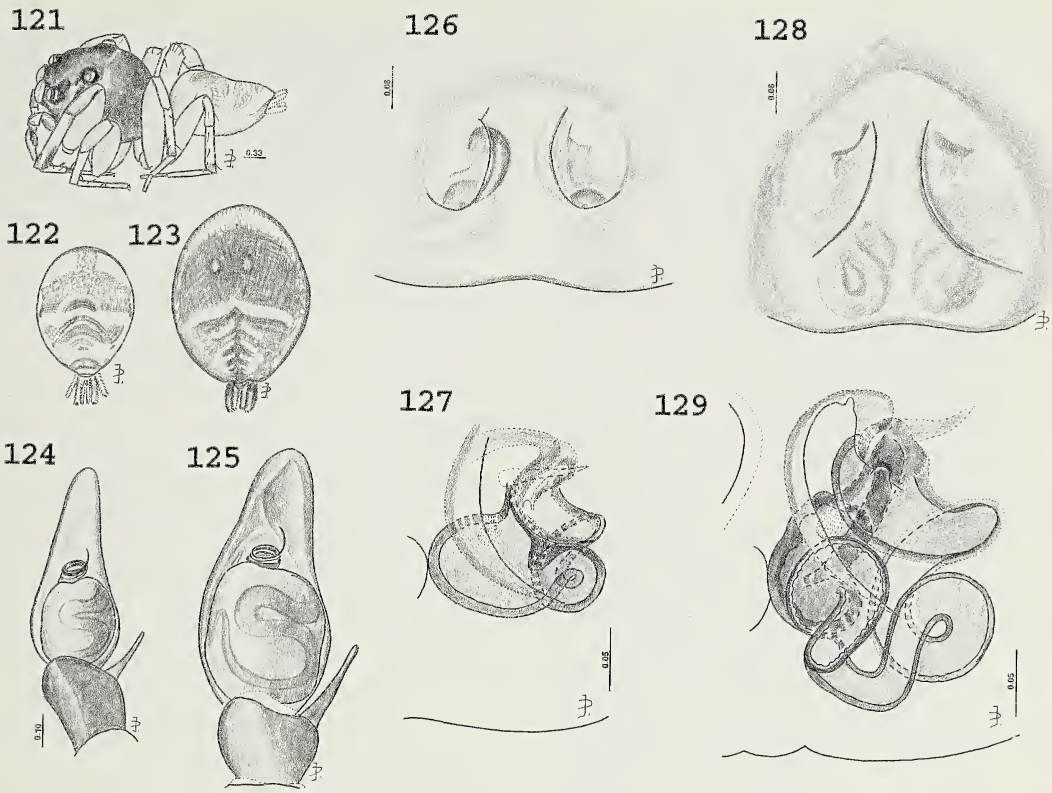
Descriptive notes.—Carapace with anterior swelling below second eye row, sides of carapace anteriorly parallel, eye field almost square, indistinctly shorter than broad, with flat area extending slightly behind eye field, posterior slope steep, relatively high. Abdomen oval, broad, but not broader than carapace, somewhat flattened, darkly pigmented with a pattern of white anterior edge and transverse lines in the posterior half. *Legs:* Robust and long, leg formula in males 1-3≥4-2, in females 4=3-1-2. *Palp:* of euophryine type, characterized by long apex of cymbium, embolus making a small, very tight and narrow coil atop bulb, tibia short, apophysis narrow and set diagonally, about half the length of the bulb. *Epigynum:* with two anterior grooves, separated by narrowing ridge, spermatheca relatively large, and duct sclerotized, broad and making complicated bends, opening almost invisible, even after clearing.

Map 8.—Distribution of *Zenodorus microphthalmus* (★) (known from throughout the Pacific) and ***Zenodorus ponapensis*** new species (■), known only from Ponape in the Caroline Islands.

Zenodorus microphthalmus (L. Koch 1881) NEW COMB.
Figs. 123, 125, 128, 129; Map 8

Jotus microphthalmus L. Koch 1881.
Mollica microphthalma: (L. Koch): Simon 1900.

Description.—*Male* and *female:* Sexes very similar. Carapace blackish-brown with lighter area on anterior thorax, eye field darker, finely rugose with indistinct sparse, small dark setae, sparse white scales around lateral and posterior edges of eye field. Abdomen dark grey, indistinctly spotted lighter, with broad white belt along anterior edge and thin transverse line, interrupted medially; there are smaller lateral markings in front of spinnerets; these white areas are devoid of pigmentation and covered with whitish scales, sparse whitish scales occur also on grey areas, intermixed with small brown setae and bristles. Frontal view with strong contrast between intensely black chelicerae and dark, bare clypeus and white belt of setae running laterally from AME and under ALE; thin line of white setae surrounding eyes I, dark face contrasts also with the largely yellowish legs. Chelicerae also black in female but face brown, whitish setae more sparse and less prominent than in male, legs I and pedipalps brown. One retrolateral cheliceral tooth, one



Figures 121–129.—Comparison of the widely distributed species *Zenodorus microphthalmus* with ***Zenodorus ponapensis*** new species from Ponape in the Caroline Islands. 121, General appearance of male of ***Zenodorus ponapensis*** new species; 122, Abdominal pattern in female of ***Zenodorus ponapensis*** new species; 123, Abdominal pattern in female of *Z. microphthalmus*; 124, Palpal organ ventrally in ***Z. ponapensis*** new species; 125, Palpal organ ventrally in *Z. microphthalmus*; 126, Epigynum in ***Z. ponapensis*** new species; 127, Internal structure of epigynum showing single spermatheca and ducts in ***Z. ponapensis*** new species. 128, Epigynum in *Z. microphthalmus*; 129, Internal structure of epigynum showing single spermatheca and ducts in *Z. microphthalmus*.

(bicusp) prolateral cheliceral tooth. Ventral view shows mouth parts blackish-brown, sternum brown, coxae greyish-brown, abdomen dark brownish-grey with four thin, light longitudinal lines. *Legs:* In female dark brown, in male more differentiated, light greyish-yellow, with dark brown tibiae I-IV, apical halves of femora III-IV and parts of some other segments. Ventral spines of tibia I: outer row, 3; inner row, 3; with spination indistinct, almost invisible among long and dark setae. *Palp:* Bulb larger and tibial apophysis longer than in *Z. ponapensis* (Fig. 125). *Epigynum:* Sclerotized duct makes 4–5 complicated bends (Figs. 128, 129).

Material examined.—FIJI: *Viti Levu*, Nausori Highlands, forest reserve, Koronsingalevu Block, elev. 1500 ft., sweeping/shaking, 1♂1♀, 27 May 1987 (JWB & ERB). Nandarivatu, on garage, 1♀1imm, 12 April 1987 (JAB). Nandarivatu, in house, 1♀2imm, 11 April 1987 (JAB). Nandarivatu, night-lighting around house, 1♀, 14 May 1987 (JWB). **CAROLINE ISLANDS**: *Palau*, Babelthuap, Ngaremlengui, 2♀, 21 April 1973 (JWB & JAB). Babelthuap, Airai, mixed tropical forest, woods below SDA school, 1♀, 11 March 1973 (JWB & JAB). Rock island east of Malakal, tree shaking, 1♀1imm, 12 February 1973 (JWB). Rock island east of Malakal, betel palm trash, 1♂5imm, 8 March 1973 (JWB & JAB). Angaur, mixed tropical forest, tree shaking, 1♀, 30 April 1973 (JWB, ERB & JAB). Angaur, in *Triumfetta* litter on beach, 1♀, 27 April 1973 (JWB, ERB & JAB). Angaur, under *Casuarina* bark, 2♂3♀8imm, 29 April 1973 (JWB, ERB & JAB). Angaur, *Casuarina* litter near beach, 1♂2imm, 29 April 1973 (JWB, ERB & JAB). Angaur, banana/palm thicket, 1♂4imm, 29 April 1973 (JWB, ERB & JAB). Angaur, in house,

1♂, 30 April 1973 (JWB, ERB & JAB). *Truk*, Moen Island, tree shaking, 1♂, 12 June 1973 (JAB & JWB). **MARSHALL ISLANDS**: *Kwajalein Atoll*, Ennylebegan Islet, shaken from trees, 1♂, 21 July 1969 (JWB). **NEW CALEDONIA**: *Loyalty Is.*, Lifou, 1♂, 26–28 March 1968 (J.L. Gressitt & T.C. Maa) (BPBM). We Lifou, 1♀, February 1962 (N.L.H. Krauss) (BPBM). Hienghene, 0–50 m, 1♀, January 1969 (N.L.H. Krauss) (BPBM). Mt. Ponie, 100-400 m, 1♀, February 1974 (N.L.H. Krauss) (BPBM). **VANUATU (= NEW HEBRIDES)**: *Efate Is.*, Port Vila, 0–100 m, 1♂, December 1983 (N.L.H. Krauss) (BPBM). *Santo Is.*, Big Bay, elev. 0–30 m, Acc #1979.380, 1♀, 10 September 1979 (W.C. Gagne) (BPBM). 15 km N of Luganville, 100 m, Acc. #1979.360, 12 September 1979 (W.C. Gagne) (BPBM). **NEW GUINEA**: *Wau*, 1200 m, 1♂, 25 December 1961 (J. Sedlock) (BPBM). **SOLOMON ISLANDS**: *Guadalcanal*, Honiara, 100 m, 1♀, December 1971 (N.L.H. Krauss) (BPBM). Bougainville, S Kokure nr. Crown Prince, ca. 900 m, 1♀, 8 June 1966 (J.L. Gressitt) (BPBM). Kokure, Bougainville, 690 m, 1♀, 12 June 1956 (E.J. Ford, Jr.) (BPBM). **HAWAIIAN ISLANDS**: *Hawaii County*, Manuka State Park, mesic forest, elev. 1750 ft., 1♂2♀4imm., 11 February 1995 (JWB & ERB); Palani Road 1 mi. N of Kalua, desert shrubs, 1♀ 17 February 1995 (JWB & ERB); Manuka State Park nature trail, 1♂, 19 February 1995 (JWB & ERB); Puna District, Lava Tree State Park, 1♀2imm., 25 February 1995 (JWB & ERB).

Distribution.—Known from many islands throughout the Pacific Ocean.

Zenodorus ponapensis new species
Figs. 121, 122, 124, 126, 127; Map 8

Holotype.—Male from Caroline Islands, Ponape, palm forest E of Kolonia, 200 ft. elev., 5 June 1973 (JAB & JWB) (BPBM).

Etymology.—This species is named after Ponape, the only island on which it has been found.

Diagnosis.—Palpal organ smaller than in *Z. microphthalmus*, cymbium longer, pronouncedly narrowing anteriorly, epigynum smaller with median septum not narrowing anteriorly, copulatory duct short in proportion to spermatheca, and making two or three bends (Figs. 124, 125).

Description.—Both sexes very similar. Carapace brown, eye field darker, finely rugose with indistinct, sparse, small dark setae, sparse white scales around lateral and posterior edges of eye field. Light areas covered with colorless scales; whole abdomen with sparse, small brown setae and bristles. Frontal view shows contrast between black-brown chelicerae together with brown face and largely light yellow legs. Sparse white spots of single setae scattered over face and edge of clypeus. Female with a lighter brown face and uniformly yellow legs. Ventral view has mouth parts brown, sternum brown, darker marginally, coxae whitish. Abdomen has pattern comparable with *Z. microphthalmus;* medially grey with broad whitish-yellow marginal streak.

Male: (n = 5). Total length 3.8–4.4 ($\bar{x}$ = 4.10), length of carapace 2.0–2.4 ($\bar{x}$ = 2.25), maximum carapace width 1.5–1.7 ($\bar{x}$ = 1.61), eye field length 0.9–1.1 ($\bar{x}$ = 1.07), eye row I width 1.5 ($\bar{x}$ = 1.50). One retrolateral cheliceral tooth, one (bicusp) prolateral cheliceral tooth. *Legs:* Leg formula 1-3-4-2; patella-tibia I length 1.1–1.8 ($\bar{x}$ = 1.62), with patella-tibia III equal to IV. Ventral spines of tibia I: outer row, 2; inner row, 2–3 (third spine, when present, weak). Legs II-IV yellow, legs I more differentiated, yellow with dark brown areas on patella, tibia and metatarsus. *Palp:* Apex of cymbium thinner and longer than in *Z. microphthalmus* (Figs. 124, 125).

Female: (n = 5). Total length 4.6–5.9 ($\bar{x}$ = 5.25), length of carapace 2.0–2.6 ($\bar{x}$ = 2.40), maximum carapace width 1.7–2.0 ($\bar{x}$ = 1.84), eye field length 1.1–1.3 ($\bar{x}$ = 1.25), eye row I width 1.6–1.8 ($\bar{x}$ = 1.68). Cheliceral teeth as in male. *Legs:* Leg formula 4=3-1-2; patella-tibia I length 1.4–1.7 ($\bar{x}$ = 1.57);, patella-tibia III longer than IV. Legs uniformly yellow. Ventral spines of tibia I as in male. *Epigynum:* sclerotized duct makes two or three bends (Figs. 126, 127).

Material examined.—CAROLINE ISLANDS: *Ponape*, E of Kolonia, palm forest, 200 ft. elev., 4♂(including holotype)3♀10imm, 5 June 1973 (JAB & JWB). SW of Sekere school, bushes/bank, 5♀9imm, 10 June 1973 (JWB & JAB). Nanpil, vegetation half-way up hill, 1♀1imm, 6 June 1973 (JAB & JWB). Sokehs I., shaking in banana/breadfruit, 1♂2♀2imm, 9 June 1973 (JWB & JAB). Top of mountain, tree shaking, 4♂3imm, 6 June 1973 (JAB & JWB). Tolotom, 2100 ft., 1♂, 26 August 1950 (P.A. Adams) (BPBM).

Distribution.—Known only from the island of Ponape in the Caroline Islands.

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A NEW GENUS AND SPECIES OF THERAPHOSID SPIDER FROM BELIZE (ARANEAE, THERAPHOSIDAE)

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ABSTRACT. A monotypic theraphosid spider genus, ***Crassicrus*** new genus, and a new species ***Crassicrus lamanai*** new species, are described from the tropical dry forest of north-central Belize. Natural history and biogeographical notes are given.

The mygalomorph family Theraphosidae is a large and diverse group which is poorly known, particularly in Belize. Belizean material collected by E.C. Welling M. in 1984 and sent to the second author included six specimens that did not fit any known theraphosid genus. Examination of these specimens suggested that they represented a new genus within the theraphosid subfamily Theraphosinae, as they exhibited the large subtegulum diagnostic of that subfamily (Raven 1985). Mature males collected by the first author in 1995 confirmed the existence of a locally abundant and distinctive new genus of theraphosid spider, described below, from the dry tropical forest of northern Belize.

METHODS

All measurements are in mm and were made using a dial caliper, ±0.01 mm. Leg and pedipalp measurements were made on the left side of all specimens. Trochanters and coxae were measured from their ventral aspect, while all other leg measurements were taken dorsally. Leg segment widths were measured dorsoventrally at the point of greatest width. The spermathecal illustration was based on stereomicroscopic examination of dissected spermathecae. Spination abbreviations follow Prentice (1992). Standard abbreviations are used for ocular descriptions. Coloration was recorded during examination of live specimens under sunlight using color charts from the Pantone Book of Color (Eisman & Herbert 1990).

Crassicrus new genus

Type species.—*Crassicrus lamanai* new species.

Etymology.—From the Latin root *crass*, thick, and *crus*, shin, in reference to the incrassate tibia of leg IV.

Diagnosis.—*Crassicrus* possesses a more incrassate, barrel-shaped tibia IV than *Eupalaestrus* Pocock 1901, the only other New World theraphosid to exhibit this feature. This character state is present in both sexes but more pronounced in the female. *Crassicrus*, in contrast to *Eupalaestrus*, lacks a scopulated pad on the retrolateral surface of femur IV. Females are readily distinguished from all other theraphosids by a field of thorn-like setae on the entire ventral and ventro-prolateral surface of coxae and femora II-IV. Both sexes possess fine plumose hairs on the retrolateral surface of the palp trochanter and femur and the opposing prolateral surface of the leg I trochanter and femur.

Included species.—Only the type species.

Crassicrus lamanai new species
Figs. 1–9; Tables 1–4

Types.—Holotype male, paratype female from 0.5 km W New River Lagoon, Indian Church Village near Lamanai Forest Reserve, Orange Walk District, Belize, 6 January 1995 (S.B. Reichling). *Paratypes:* 7 January 1995,

1♂ (S.B. Reichling); 3 September 1995, 2♂ (S.B. Reichling). 9 January 1995, 4♀ (S.B. Reichling). Locality for all paratypes as above. All specimens deposited in the American Museum of Natural History, New York.

Etymology.—The specific epithet is a noun in apposition from the Mayan word *lama' anayin*. This was the name of their ancient trading center, still standing centuries later, but now called Lamanai.

Diagnosis.—The diagnostic generic characters of the monotypic *Crassicrus* also serve to distinguish the species ***Crassicrus lamanai*** new species. The morphology of the male palpal bulb is diagnostic in that the apex exhibits 5–6 prominent keels. The mature male is further distinguished from most other theraphosids by the swollen third tibia. In addition, female *C. lamanai*, when freshly molted, exhibit a distinctive anterior to posterior two-toned coloration.

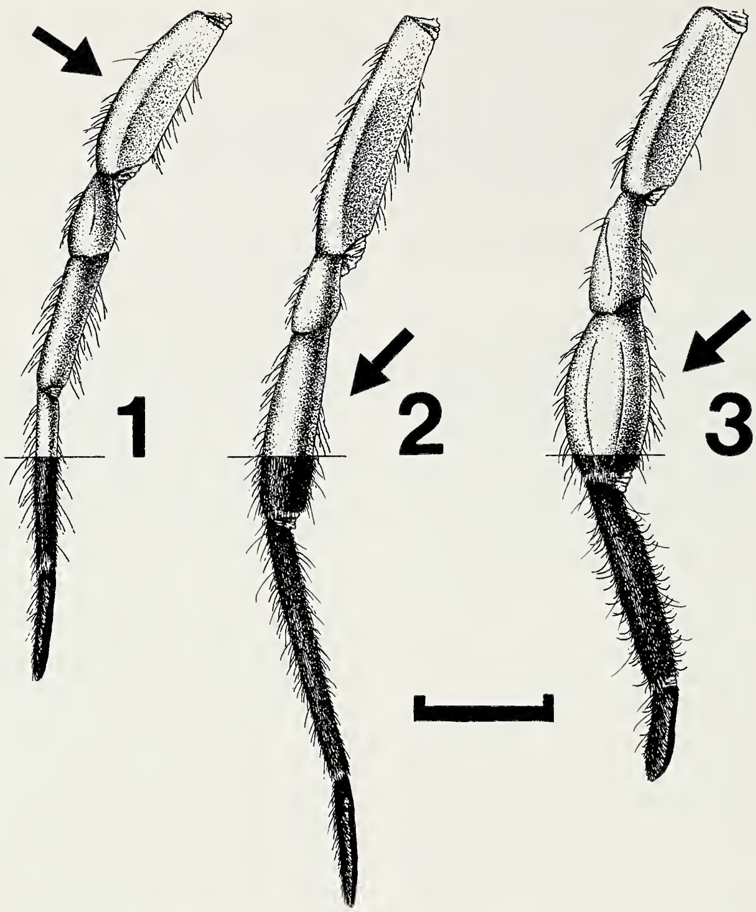
Description.—*Male (holotype):* Length 36.9. Carapace length 16.3, width 14.1, carapace width/length 0.86; chelicerae, width 5.6; right fang furrow, 12 macroteeth, left furrow damaged; sternum, width 6.1, sternum length 6.8; sigilla at base of coxae I, II, and III, posterior pair largest. Labial cuspules, 56, medial anterior face; maxillary cuspules, 199, 188, baso-prolateral surface. Leg span, measured from apex of left tarsus I to apex of left tarsus IV, 136.7. Femur III moderately incrassate, maximum width 3.5 (Fig. 1); femora I, II, and IV, 2.0, 1.9, and 2.7, respectively. Tibia IV slightly incrassate, maximum width 2.5 (Fig. 2); tibiae I, II, and III, 1.5, 1.8, and 1.5, respectively; maximum width tibia IV/maximum width femur IV 0.81. Leg and palp segment lengths in Table 1.

Entire spider shiny black with deep violet pubescence when viewed in strong light. Maxillary hairs dull orange. Carapace clothed in sparse covering of jet black (Pantone, 19–0303) hairs. Abdomen clothed in short, jet black hairs interspersed with longer jet black setae; pubescence dense over posterior half of abdomen dorsum, corresponding to circular patch of type I (Cooke et al. 1972) urticating hairs; pubescence over anterior half of abdomen sparse, with integument clearly visible. Legs hirsute and jet black; short pubescence with abundant long setae on all segments.

Carapace lacking pronounced bosses; caput not markedly elevated; fovea deep and weakly procurved. Anterior eye row procurved; AME round, diameter 0.5, separated by 0.2; ALE ovoid, 0.3 × 0.4. Posterior eye row crescentic; PME ovoid, 0.1 × 0.2; PLE ovoid, 0.2 × 0.3, separated by 0.9. Clypeus very narrow. Tibia I with usual bipartite spur; shorter upper process with one preapical ventral megaspine; longer lower process strongly curved toward upper process, one subapical megaspine on surface facing upper spur (Fig. 4). Coxae without plumose setae; short, spiniform setae on anterior face of coxae I and II. Trochanters of femora I and II with fine plumose hairs on prolateral face. Long setae interspersed abundantly within short pubescence on all leg segments. Tarsal scopulation complete and entire. Metatarsal scopulation entire: I, complete; II, 0.67; III, 0.48; IV, 0.14. Basal portion of middle division of palpal bulb broad with concave ventral region angled abruptly downward, somewhat less than 90°, with six prominent keels spiraling to broadly truncated apex; single dorsal keel serrated (Figs. 5, 6). *Spination:* Leg I, metatarsus 1v(am), tibia 3v(2ap 1ar); leg II, metatarsus 1d(br) 3v(1am 1m0.71 1br), tibia 6v(2ap 1am 1m0.43 1m0.35 1bm); leg III, metatarsus 9v(3ap 1am 1ar 1er 1m0.30 1r0.30 1bm), tibia 2v(1m0.50 1bm), femur 1d(ep); leg IV, metatarsus 4d(1am 1ap 1ep 1p0.60) 5v(1am 1m0.70 1m0.45 1m0.21 1bm), tibia 2d(1am 1em) 2v(1am 1bm); palp, tibia 4v(2ap 1ep 1bp).

Female (paratype): Length 48.9. Carapace length 22.2, width 18.0, carapace width/carapace length 0.81; chelicerae, width 9.3; right fang furrow, 13 macroteeth, left furrow, 14 macroteeth; sternum, width 7.2, length 10.6; sigilla as in holotype. Labial cuspules, 82, medial anterior face; maxillary cuspules, 234, 233, baso-prolateral surface. Leg span, 126.8. Tibia IV overtly incrassate, maximum width 5.3 (Fig. 3); tibiae I, II, and III, 3.2, 3.6, and 3.4, respectively; maximum width tibia IV/maximum width femur IV 1.22. Leg and palp segment lengths in Table 2.

Overall brown dorsally, with pronounced anterior to posterior difference in shade. Medium brown anteriorly (carapace, chelicerae, patellae, tibiae, metatarsi and tarsi I, II, and palp), distinctly darker shades posteriorly (abdomen, legs III and IV). Ventral aspect also distinctly bi-toned, leg IV and abdomen dark brown to black. Coloration in preservative uniform dark brown. Chelicerae clothed in

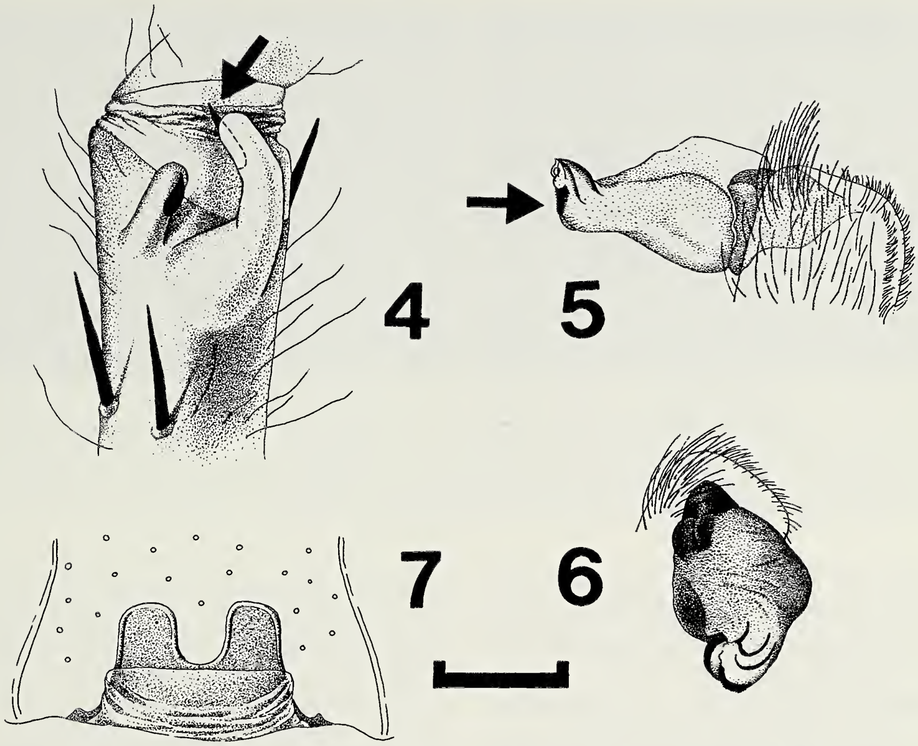


Figures 1–3.—***Crassicrus lamanai*** new genus and new species. 1, Male holotype, leg III, retrolateral view, showing moderately incrassate femur (arrow); 2, Male holotype, leg IV, retrolateral view, showing weakly incrassate tibia (arrow); 3, Female paratype, leg IV, retrolateral view, showing strongly incrassate tibia (arrow). All legs depicted with setae removed from proximal ¾ to highlight segment morphology. Scale line = 1 cm.

Table 1.—***Crassicrus lamanai*** new genus and new species. Male holotype; length of leg and pedipalp segments (mm).

Leg	I	II	III	IV	Palp
Coxa	7.3	7.3	6.0	6.0	4.0
Trochanter	2.1	2.4	2.0	2.7	1.2
Femur	15.3	14.6	12.3	16.0	8.9
Patella	8.1	7.0	6.0	6.7	5.5
Tibia	11.6	11.0	10.4	13.5	8.0
Metatarsus	12.2	12.0	13.1	18.3	—
Tarsus	8.5	7.9	7.0	8.6	3.4
Total length	65.1	62.2	56.8	71.8	31.0

tortoise-shell brown (Pantone, 19–1241) pubescence with longer setae of similar color but basal ⅓ grading to black. Maxillary hairs dull orange. Carapace clothed in short, dense tortoise-shell brown pubescence, closely appressed. Abdomen with velvety, dense pubescence interspersed with long setae; dorsum bracken brown (Pantone, 19–1015) with persimmon orange (Pantone, 16–1356) setae; ventral pubescence and setae rich jet black; sharp basolateral division between dorsal and ventral coloration; urticating hair patch of type I hairs covering posterior half of abdomen dorsum with crescentic anterior margin. Coxae and trochanters of all legs except IV dark earth brown (Pantone, 19–1012). Femora I, II, III, and palpal femur distinctly darker



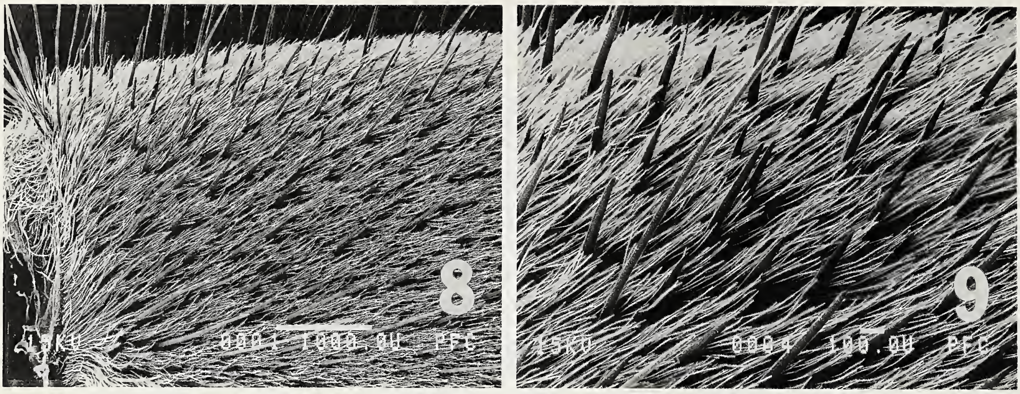
Figures 4–7.—***Crassicrus lamanai*** new genus and new species. 4, Male holotype, left tibia I, prolateral view, showing spur processes and megaspine (arrow) location; 5, Male holotype, left palpal organ, prolateral view, showing position of serrated keel (arrow) and abruptly angled embolic region; 6, Male holotype, right palpal organ, frontal view, illustrating six spiraling apical keels; 7, Female paratype, spermathecae, dorsal view. Scale line = 2 mm.

shade than distal segments; dorsal aspect bracken brown, ventral aspect dark earth brown. Dorsal aspect of patellae, tibiae, metatarsi, and tarsi I–III and corresponding palpal segments tortoise-shell brown, ventral aspect toffee brown (Pantone, 18–1031). Leg IV entirely bracken brown.

Carapace similar to holotype but with caput more distinctly elevated; fovea as in holotype. Anterior eye row slightly procurved, less so than in holotype; AME round, diameter 0.7, separated by 0.3; ALE ovoid, 0.3 × 0.6. Posterior eye row crescentic; PME round, diameter 0.3; PLE ovoid, 0.3 × 0.4, separated by 1.3. Clypeus absent. Coxae without plumose setae; short, spiniform setae on coxae I and II as in holotype. Trochanters of femora I and II with fine plumose hairs as in holotype. Femora II–IV with numerous thorn-like setae along entire ventral and ventro-prolateral surface (Figs. 8, 9). Tarsal scopulation complete and entire. Metatarsal scopulation entire: I, complete; II, 0.87; III, 0.65; IV, 0.18. Spermathecae discrete, a broad low mound with two compact lobes, total width at base 2.5; lobes without basal taper and proximally connected for half their length, free extension of lobes 0.8 long (Fig. 7). *Spination:* Leg II, tibia 1d(p0.66) 1v(ap); leg III, metatarsus 7v(2am 1ar 1r0.46 1m0.46 1m0.45 1br), tibia 6v(2am

Table 2.—***Crassicrus lamanai*** new genus and new species. Female paratype; length of leg and pedipalp segments (mm).

Leg	I	II	III	IV	Palp
Coxa	8.5	7.5	7.4	8.3	6.5
Trochanter	2.3	1.7	3.2	3.8	1.5
Femur	15.4	14.1	12.9	16.5	11.3
Patella	9.2	8.2	7.7	9.2	6.6
Tibia	10.0	9.1	7.7	12.3	7.9
Metatarsus	9.9	9.0	10.8	14.6	—
Tarsus	7.0	7.0	6.1	6.5	7.3
Total length	62.3	56.6	55.8	71.2	41.1



Figures 8, 9.—***Crassicrus lamanai*** new genus and new species. Female from 5 km S Belmopan, Cayo District, Belize, scanning electron micrographs of femur III, ventro-prolateral view. 8, Showing distribution and density of thorn-like setae on basal portion of segment; 9, Detail of thorn-like setae emerging through pile hairs. Scale line in Fig. 8 = 1 mm, scale line in Fig. 9 = 0.1 mm.

1er 1r0.55 1r0.21 1m0.21); leg IV, metatarsus 13v(2am 2ap 1er 2m0.73 2m0.63 1m0.58 1m0.52 2m0.36), tibia 3v(2ar 1ap); palp, tibia 1d(ap) 7v(2ap 2ar 2ep 1b).

Variation.—*Males (four, including holotype):* Length, range (mean ± SD) 36.6–40.1 (38.0 ± 1.6), carapace length 16.3–17.3 (16.7 ± 0.4), width 13.9–15.7 (14.8 ± 0.9), carapace width/length 0.84–0.92 (0.88 ± 0.04); three specimens with 11 or 12 macroteeth (10, 11 in one individual). Labial cuspules 24–64 (52 ± 19); maxillary cuspules 134–199 (174 ± 20) per maxilla. Leg span 131.7–152.5 (142.4 ± 9.8). Tibia IV weakly-to-moderately incrassate in all specimens examined, maximum width 0.74–0.98 (0.84 ± 0.1)× maximum width of femur IV. Variation in leg and palp segment lengths in Table 3. Extent of metatarsal scopulation: I, fully scopulate on all specimens; II, 0.67–0.83 (0.76 ± 0.07); III, 0.47–0.61 (0.50 ± 0.07); IV, 0.14–0.26 (0.19 ± 0.05). Palpal embolus morphology uniform with regard to the presence of spiraling apical keels, but keel number varied from 5–6 (two individuals respectively).

Females (five): Length 43.9–51.1 (48.5 ± 3.0), carapace length 15.2–22.0 (19.2 ± 2.7), width 13.5–18.5 (16.7 ± 2.0), carapace width/length 0.81–0.89 (0.87 ± 0.03). Most specimens with 13 or 14 macroteeth (12, 14 in one individual). Labial cuspules 82–122 (98 ± 16); maxillary cuspules 202–290 (236 ±

Table 3.—***Crassicrus lamanai*** new genus and new species. Four males including holotype; range (mean ± SD) of log and pedipalp segment lengths (mm).

Leg	I	II	III	IV	Palp
Coxa	7.3–7.9 (7.5 ± 0.3)	6.5–7.4 (7.0 ± 0.4)	5.6–6.4 (6.0 ± 0.3)	5.8–7.4 (6.5 ± 0.7)	4.0–6.0 (4.7 ± 0.9)
Trochanter	1.3–2.7 (2.2 ± 0.7)	2.4–3.0 (2.7 ± 0.3)	2.0–3.5 (2.7 ± 0.8)	2.3–3.3 (2.7 ± 0.4)	1.2–2.7 (2.1 ± 0.6)
Femur	15.1–16.5 (15.8 ± 0.7)	14.4–15.8 (15.2 ± 0.8)	12.3–14.2 (13.0 ± 0.8)	14.1–17.8 (16.1 ± 1.5)	8.9–10.0 (9.4 ± 0.5)
Patella	7.4–8.3 (8.0 ± 0.4)	6.9–7.6 (7.2 ± 0.4)	6.0–7.0 (6.5 ± 0.4)	6.3–7.7 (7.0 ± 0.6)	5.1–6.2 (5.6 ± 0.4)
Tibia	11.6–14.0 (13.2 ± 1.1)	11.0–12.7 (11.9 ± 0.9)	9.7–11.2 (10.6 ± 0.7)	13.5–15.7 (14.6 ± 1.1)	7.4–9.0 (8.2 ± 0.7)
Metatarsus	11.3–12.2 (11.8 ± 0.4)	10.1–12.0 (11.2 ± 0.8)	11.1–13.1 (12.0 ± 0.8)	14.4–18.3 (16.8 ± 1.7)	—
Tarsus	8.5–9.7 (9.0 ± 0.6)	7.9–9.0 (8.6 ± 0.5)	7.0–8.8 (8.2 ± 0.8)	8.6–9.8 (9.4 ± 0.5)	2.4–3.8 (3.1 ± 0.6)

Table 4.—*Crassicrus lamanai* new genus and new species. Five female paratypes; range (mean ± SD) of leg and pedipalp segment lengths (mm).

Leg	I	II	III	IV	Palp
Coxa	6.6–9.4 (8.1 ± 1.0)	6.4–8.4 (7.3 ± 0.7)	5.4–7.4 (6.7 ± 0.8)	6.4–8.3 (7.6 ± 0.8)	4.7–6.5 (5.8 ± 0.8)
Trochanter	1.9–3.1 (2.4 ± 0.5)	1.7–2.3 (2.0 ± 0.2)	1.8–3.2 (2.3 ± 0.6)	2.4–3.8 (2.8 ± 0.8)	1.5–2.8 (2.0 ± 0.5)
Femur	12.8–15.9 (14.6 ± 1.4)	12.2–14.6 (13.5 ± 1.2)	10.9–13.7 (12.2 ± 1.3)	13.6–16.9 (15.6 ± 1.4)	8.8–11.5 (10.3 ± 1.2)
Patella	6.8–9.5 (8.5 ± 1.1)	6.5–8.5 (7.7 ± 0.8)	5.9–8.4 (7.3 ± 0.9)	6.8–9.2 (8.2 ± 0.9)	5.6–6.7 (6.4 ± 0.4)
Tibia	8.6–11.5 (10.3 ± 1.1)	8.7–10.4 (9.6 ± 0.7)	7.7–9.8 (8.8 ± 0.9)	11.8–14.0 (13.1 ± 1.0)	5.7–7.9 (7.1 ± 0.9)
Metatarsus	7.2–9.9 (8.3 ± 1.1)	6.6–9.0 (8.0 ± 0.9)	6.9–10.8 (8.7 ± 1.5)	10.2–14.6 (12.4 ± 1.6)	—
Tarsus	5.7–7.3 (6.8 ± 0.6)	5.9–7.2 (6.6 ± 0.5)	6.1–7.4 (6.7 ± 0.6)	6.5–8.4 (7.5 ± 0.8)	6.4–7.7 (7.2 ± 0.5)

24) per maxilla. Leg span 112.6–140.5 (127.3 ± 10.5). Tibia IV strongly incrassate in all adult specimens examined, maximum width 1.22–1.24 (1.23 ± 0.01)× maximum width of femur IV. An ontogenetic trend in the relative width of tibia IV; one subadult (leg span 112.6) with maximum width 1.12× maximum width of femur IV and juveniles examined in the field without incrassate podomeres. Variation in leg and palp segment lengths in Table 4. Characteristic two-toned coloration of freshly molted specimens fading to uniform tortoise-shell brown as ecdysis approaches. Extent of metatarsal scopulation: I, fully scopulate on all specimens; II, 0.73–0.81 (0.80 ± 0.05); III, 0.51–0.65 (0.58 ± 0.05); IV, 0.18–0.29 (0.24 ± 0.05). No variation in spermathecae observed.

Distribution.—At this time, *Crassicrus lamanai* new species is only known from Belize. Specimens have been collected in the north near Lamanai Forest Reserve, Orange Walk District, southward along the W bank of the New River Lagoon, and in the Cayo District, off the Hummingbird Highway. The northern half of Belize consists of low-lying hills, flat plains and swamps. The terrain changes dramatically in the southern half of Belize. A northern extension of the Maya Mountains known as Mountain Pine Ridge plateau transects the country in an east-west direction. Similar habitat to the north and northwest of the type locality suggest that *C. lamanai* may occur in Guatemala and Mexico.

Natural history.—The local Creole Indians call this species "antelope spider" based on the mistaken belief that the swollen rear legs allow it to jump great distances (E.C. Welling M., pers. comm.). Typical habitat is open areas, including man-made clearings such as corn and banana plantations. Despite intensive effort, *C. lamanai* was not found in areas of undisturbed forest where the tree canopy obscured direct sunlight from reaching the ground. This species appears to avoid shaded areas in favor of open, sunny terrain. Burrows were located in sunny clearings, often beneath partially buried limestone boulders. Soil at the type locality consisted of a layer of humus overlying a marl bed. In a random sample (n = 6) of burrows examined during September 1995, entrance width ranged from 17.8–46.1 (33.1 ± 10.7) and length ranged from 120.0–469.0 (298.7 ± 114.9). Burrows were straight with angle of descent nearly perpendicular to the ground surface plane, and were restricted to the humus overlayer.

Crassicrus lamanai is active throughout the year, except during the time immediately preceding ecdysis and while guarding eggs, at which time the burrow entrances are occluded with a soil plug, as described by Minch (1979) for *A. chalcodes* Chamberlin 1940. During daylight hours, the entrances of active burrows are draped with a thin sheet of silk. At night the spiders are at the burrow entrance, facing outward with legs I and II extended outside the burrow. Mature males begin appearing in late June and are abundant by late September.

Females visibly heavy with ova were collected during January; but specimens examined in May, July and September were thin and did not appear to contain eggs. Oviposition occurred in the laboratory during March. Ootheca were impregnated with a dense covering of abdominal hairs, similar to the behavior reported by Marshall & Uetz (1990) for *Megaphobema* (Pocock 1901). Eggs laid in captivity failed to hatch. Exact egg counts were not made, although large females were estimated to lay 350–400 eggs.

Crassicrus lamanai is sympatric with *Brachypelma vagans* (Ausserer 1875). Burrows of these two species were often found in the same open habitat with intermixed burrow aggregations composed of both taxa.

DISCUSSION

The most striking feature of *C. lamanai* is the very incrassate, barrel-shaped tibia IV. *Eupalaestrus* from SE South America is the only other Western Hemisphere theraphosid genus to have this apomorphic feature (Pocock 1901; Bucherl 1947; Raven 1985; Perez-Miles 1992). However, the potential affinity between these two genera is uncertain. While both *Crassicrus* and *Eupalaestrus* have all tarsal scopulae entire, only the latter possess a scopulated pad on the retrolateral surface of femur IV. *Crassicrus* have only type I urticating hairs while *Eupalaestrus* possess type I and II (Perez-Miles 1992) urticating hairs on the abdomen. Additionally, female *Crassicrus* possess short, thorn-like setae on the entire ventral and ventro-prolateral surface of both coxae and femora II–IV, with number and stoutness increasing from legs II–IV. This is considered here to be an autapomorphic generic feature.

Crassicrus lamanai is sympatric with the theraphosine genus *Brachypelma* Simon 1891. Smith (1994) mentioned fine plumose hairs on leg I trochanter and femur in *Brachypelma*, but failed to describe where they were situated. Examination of *B. auratum* Schmidt 1992, *B. smithi* (F.O.P.-Cambridge 1897) and *B. vagans* revealed that the fine plumose hairs occur on the retrolateral palp trochanter and femur as well as on the opposing prolateral leg I trochanter and femur. In contrast, both male and female *Crassicrus* possess plumose hairs on the prolateral face of trochantera and femora I and II.

Material examined.—The type specimens and the following: **BELIZE**: *Cayo District*: 5.0 km S Belmopan (Hummingbird Hwy.), 23 November 1984, 6♀2imm, E.C. Welling M. (RCW Col.); 12 February 1988, 4♀1imm, E.C. Welling M. (RCW Col.); 30 June 1991, 1♂1subad♂, E.C. Welling M. (RCW Col.).

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RESEARCH NOTE

INTERPOPULATION AND INTERSEXUAL VARIATION IN PECTINE TOOTH COUNTS IN *CENTRUROIDES VITTATUS* (SCORPIONIDA, BUTHIDAE)

The pectines of scorpions are comblike structures whose primary functions seem to be as contact chemoreceptors and mechanoreceptors (Hjelle 1990). These appendages are unique to scorpions and appear important in such activities as substrate recognition (Polis & Sissom 1990) and mate identification (Gaffin & Brownell 1992). A pectine consists of two pectens, or combs, each of which contains a variable number of pectinal teeth. These tooth counts, along with various other morphological aspects of the pectines, have been utilized as taxonomic characters, both to help separate genera or species and to distinguish between sexes within a species. In the latter situation, pectine tooth counts for males are generally higher than for females. In some cases (e.g., some *Paruroctonus* Werner 1934), male and female counts do not overlap (Sissom & Francke 1981); however, in many species there exists considerable overlap and sexual variation is seen as differences in the modal or average tooth number per comb. To date, there has been little attempt to determine statistically whether pectine tooth counts are, in fact, sexually dimorphic. Additionally, only one study of which I am aware [of *Uroctonus mordax* Thorell 1876 (Hjelle 1972)] has examined specimens from various populations within a species' range to determine whether there exists interpopulation variation in this trait; such variation may make it difficult to use pectine tooth counts to help distinguish sexes or species. For the family Buthidae, pectine tooth counts have been shown to differ statistically between males and females, with males having larger counts, for two litters of *Centruroides gracilis* (Latreille 1804) (Francke & Jones 1982), while no statistically significant intersexual variation was seen in *Tityus cambridgei* Pocock 1897 (Lourenço 1981). In this note I examine both sexual and interpopulation differences in pectine tooth counts in the buthid scorpion *Centruroides vittatus* (Say 1821) from three populations within the state of Texas.

Centruroides vittatus is a commonly encountered scorpion throughout the south central plains of the United States west of the Mississippi River, and northern México (Shelley & Sissom 1995). The sexes in this scorpion can be easily distinguished by the much longer and thinner metasomal segments of the males. For this study, individuals were collected from three populations: (1) the Chandler Independence Creek Preserve of the Texas Nature Conservancy, located at the confluence of Independence Creek and the Pecos River approximately 37 km south of Sheffield, Terrell County in west Texas; (2) Kickapoo Caverns State Park, located on the Kinney County-Edwards County border in south-central Texas; and (3) Lyndon B. Johnson National Grasslands, north of Decatur, Wise County in north-central Texas. Females from these populations are known to vary in overall body size as well as some life history traits (Brown & Formanowicz 1995). A total of 375 *C. vittatus* (213 females, 162 males; see Table 1) was collected in November 1991 (Kickapoo males only), April–June 1992 (males only), March–October 1993, April–July 1994, and July 1995 (Kickapoo males only). Scorpions were either immediately preserved (1991 and 1992 samples) or housed as described in Brown & Formanowicz (1995). Upon death or preservation of an individual, the number of teeth on each comb of the pectines was counted using an American Optical™ dissecting microscope. The sum of the tooth counts for both combs was used for all analyses. Analyses identical to those described below were performed separately for either the right or left comb count, resulting in slight changes in the calculated statistics

Table 1.—Pectine tooth count variation between sexes and among populations in the scorpion *Centruroides vittatus.* Counts are the sum of teeth on both left and right combs. Values given are means ± SD, range, and sample size *n*. *H* is a result from a Kruskal-Wallace ANOVA among populations for either males or females. *U* is a result from a Mann-Whitney *U*-test between sexes, performed within each population.

	Independence Creek	Kickapoo	Decatur	*H*	*P*
Males	51.7 ± 1.78	48.9 ± 2.01	47.5 ± 1.75	83.6	<0.0001
range	48–55	43–53	43–52		
n	57	54	51		
Females	47.8 ± 1.59	45.4 ± 1.77	43.5 ± 2.45	100.1	<0.0001
range	41–52	41–50	37–48		
n	64	88	61		
U	185	477.5	221		
P	<0.0001	<0.0001	<0.0001		

and *P*-values but no change in the overall results (these values are therefore not reported). Within each population, tooth count differences between males and females were examined using a Mann-Whitney *U*-test (Sokal & Rohlf 1981). Among population variation in tooth counts for both males and females was examined with a Kruskal-Wallace ANOVA (Sokal & Rohlf 1981). In the above tests, non-parametric tests were performed because of non-normality of some of the data. Since pectine tooth counts in *C. vittatus* do not change as an individual grows (unpubl. data), and because there were no significant differences among years for either sex from any population, data from all years were combined. All analyses were done using the STATISTICA computer package (StatSoft 1991).

For all three populations pectine tooth count was significantly greater in males than in females (Table 1). In addition, tooth counts differed significantly among populations for both males and females (Table 1). For both sexes, Independence Creek individuals had the greatest counts, followed by individuals from Kickapoo and then Decatur. A *post hoc* multiple comparison test (Daniel 1990) indicated that, for both males and females, counts were significantly different for all pairwise comparisons among populations.

Variation in pectine tooth counts also was found within individuals (Table 2). For each population, approximately half (47–55%) of the individuals had unequal numbers of teeth on each comb, with a maximum difference between combs of three. This result is similar to that found for *Centruroides gracilis*, where for two litters asymmetric and symmetric counts were equally frequent (Francke & Jones 1982). A *G*-test of independence (Sokal & Rohlf 1981) for each population indicated that sex did not influence whether individual scorpions had equal or unequal numbers of teeth per comb for Kickapoo ($G = 0.82$, $P = 0.37$) or Decatur ($G = 0.50$, $P = 0.48$), while the result was marginally significant for Indepen-

Table 2.—Within individual variation in pectine tooth counts in *Centruroides vittatus.* "Equal" indicates that both combs on an individual had the same number of teeth. "Unequal" indicates that the combs on an individual had unequal numbers of teeth. Numbers in parentheses indicate individuals that had the highest count on the left or right comb, respectively.

	Independence Creek		Kickapoo		Decatur	
	Females	Males	Females	Males	Females	Males
Equal	34	20	46	24	34	25
Unequal	30	37	42	30	27	26
	(9, 21)	(16, 21)	(14, 28)	(11, 19)	(10, 17)	(12, 14)

dence Creek ($G = 3.95$, $P = 0.047$), with males being more likely to have unequal counts. However, sex did influence which comb had more teeth. In females, the right comb was more likely than the left comb to have a greater tooth count (statistically significant for only Independence Creek and Kickapoo), while in males either comb was equally likely to have the greater tooth count [G-test for goodness of fit (Sokal & Rohlf 1981), for females—Independence Creek: $G = 5.63$, $P < 0.025$; Kickapoo: $G = 4.76$, $P < 0.025$; Decatur: $G = 1.84$, $P > 0.1$; and for males—Independence Creek: $G = 0.68$, $P > 0.1$; Kickapoo: $G = 2.16$, $P > 0.1$; Decatur: $G = 0.15$, $P > 0.5$].

These results indicate statistically that pectine tooth counts in *C. vittatus* are sexually dimorphic, and that variation in counts between combs of an individual is quite common, similar to results found in a smaller sample of the congener *C. gracilis* (Francke & Jones 1982). In addition, I have shown that variation in this trait can be observed among populations of a single species, as has been demonstrated for other traits such as body size or color patterns. This latter result illustrates the potential problems when using pectine tooth counts to distinguish sexes or species. As an example in *C. vittatus*, if a sample included only males from Independence Creek and females from Decatur, one would conclude that tooth counts were very dimorphic, with almost no overlap in the range of total tooth counts. Alternatively, if only females from Independence Creek and males from Decatur were available, one would conclude that pectine tooth counts were not sexually dimorphic, and in fact showed nearly complete overlap in total tooth counts. Both of these conclusions are potentially misleading, since an important source of variation (among populations) has not been considered.

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RESEARCH NOTE

SURAZOMUS CHAVIN NEW SPECIES, FIRST SCHIZOMIDA (HUBBARDIIDAE, HUBBARDIINAE) DESCRIBED FROM PERU

The order Schizomida is known in South America only from the northern third of the continent. There are no records from Argentina, Chile, Paraguay, or Uruguay (Reddell & Cokendolpher 1995). Although 14 species have been described from South America, many collections consist only of females and immatures and therefore have not been identified or described. Until now, the only schizomids known from Peru (from Madre de Dios, Pasco and Ucayali Departments) were identified only to subfamily (Hubbardiinae) by Reddell & Cokendolpher (1995). This paper describes a new species of *Surazomus* Reddell & Cokendolpher 1995 (formerly, *Schizomus brasiliensis* group) from Peru from adults of both sexes.

The nomenclature of flagellar setae and other anatomical terms follow that of Harvey (1992) and Reddell & Cokendolpher (1995). Acronyms of the institutions where the specimens are deposited are: AMNH (American Museum of Natural History, New York); INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus); SMNK (Staatliches Museum für Naturkunde Karlsruhe); MZSP (Museu de Zoologia, Universidade de São Paulo); MHSM, (Museo de Historia Natural da Universidade de San Marcos, Lima); TMM, (Texas Memorial Museum, Austin).

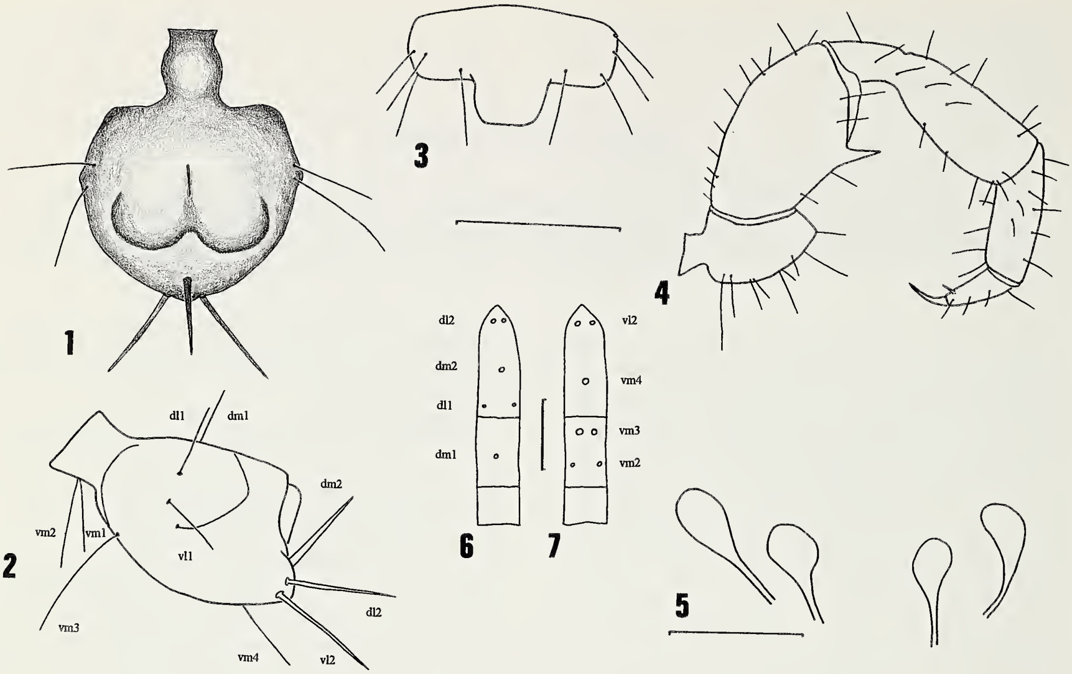
Surazomus chavin new species
(Figs. 1–7)

Etymology.—In reference to the Indian culture Chavin, that was in the area during Pre-Columbian times.

Type material.—Holotype male collected near Rio Yuyapichis, Pachitea, Panguana, Departamento Huánuco, Peru (9°37′S, 76°56′W, elev. 260 m), 3–17 December 1984 (SMNK); paratypes: 14♂ and 13♀, collected between May 1984–May 1985 (AMNH, INPA, SMNK, MZSP, MUSM, TMM), all from type locality. *Not paratypes*: 12imm collected in June-July 1984 and between October 1984–May 1985 (SMNK, MZSP).

Diagnosis.—In most respects, the new species is very similar to *Surazomus brasiliensis* (Kraus 1967). ***Surazomus chavin*** new species can be distinguished from *S. brasiliensis* by having the male pedipalpal trochanter and flagellum more rounded and propeltidium brownish (see Kraus & Beck 1967, figs. 2–5). The presence of a pedipalp femoral spur in males and unicolorous leg patellae groups the new species with *S. brasiliensis*, *S. cuenca* (Rowland & Reddell 1979), and *S. sturmi* (Kraus 1957) (see Rowland & Reddell 1979). *Surazomus chavin* has a single pit on the male flagellum and a round posteroabdominal process like *S. brasiliensis* and *S. cuenca* (double pit and truncate postero-abdominal process in *S. sturmi*). Unlike *S. cuenca* and *S. sturmi*, the new species has the metapeltidium and legs greenish like *S. brasiliensis*. The spermathecae of *S. brasiliensis* and *S. cuenca* have not been studied; but those of *S. sturmi* are like *S. chavin*.

Description.—*Male:* Propeltidium brownish, metapeltidium and tergites brownish green. Leg patellae without white, unicolorous with other leg segments. Propeltidium with three pairs of dorsal and two frontal setae. Eyespots indistinct or absent. Metapeltidium widely divided. Anterior sternum with 14 simple setae. Abdominal tergite I with 3 setae; II-VII with 2; VIII with 6; IX with 4; XII with 4 pairs of setae and well developed posterodorsal process (Fig. 3). Flagellum (Figs. 1–2) globose, with a pair of posteromedian globose lobes, 2 ventrobasal lobes; setation: 2 dorsomedian (dm1, dm2 largest), 2 dorsolateral pairs (dl1, dl2), 2 ventrolateral pairs (vl1, vl2), 6 ventral (unpaired, vm1 and vm4; paired vm2 and vm3). Chelicera: fixed finger with 6 small teeth between 2 large teeth. Pedipalpal (Fig.



Figures 1–7.—*Surazomus chavin* new species. 1–4, Male. 1, Flagellum, dorsal; 2, Flagellum, lateral; 3, Abdominal process; 4, Right pedipalp. 5–7, Female. 5, Spermathecae; 6, Flagellum, dorsal; 7, Flagellum, ventral. Scale bars = 0.5 mm for Figures 1–5; 0.1 mm for Figures 5–6.

Table 1.—Maximum and minimum measurements (mm) of 15 males and 13 females of *Surazomus chavin* new species.

		Male	Female
Carapace	Length	0.97–1.00	0.96–1.06
Flagellum	Length	0.32–0.34	0.20–0.28
	Width	0.29–0.31	—
Leg I	Femur	0.87–0.90	0.80–0.87
	Patella	1.03–1.07	0.90–0.98
	Tibia	0.71–0.73	0.63–0.71
	Basitarsus-telotarsus	0.76–0.79	0.60–0.68
Leg II	Femur	0.60–0.62	0.56–0.65
	Patella	0.34–0.36	0.27–0.34
	Tibia	0.38–0.40	0.27–0.36
	Basitarsus	0.35–0.36	0.31–0.39
Leg III	Femur	0.54–0.58	0.50–0.59
	Patella	0.27–0.29	0.18–0.25
	Tibia	0.27–0.29	0.22–0.30
	Basitarsus	0.38–0.40	0.30–0.37
Leg IV	Femur	1.00–1.03	0.81–0.89
	Patella	0.41–0.43	0.38–0.46
	Tibia	0.62–0.65	0.49–0.57
	Basitarsus	0.56–0.58	0.43–0.52

4) trochanter slightly acute apically, 1 mesal spur; femoral spur about ¼ of femur length; patella slightly constricted on dorsobasal ⅓; tarsal spurs about ⅕ of segment length; claw about ⅓ of tarsus length. Basitarsal-telotarsal articles of leg I with approximate proportions: 19-3-4-3-3-4-12. Measurements in Table 1.

Female (as male except as follows): Anterior sternum with 12 simple setae. Median and lateral spermathecae similar in size, narrowed basally, expanded to nearly circular apically, without concentration of sclerotization. Gonopod absent. Pedipalpal trochanter more rounded apically than male; femur unarmed. Basitarsal-telotarsal articles of leg I with approximate proportions: 22-3-4–4-3-4-12. Flagellum 3-segmented; setation: 5 pairs (vm2, vm3, vl2, dl1, dl2), 3 unpaired (dm1, dm2, vm4), vm2 and dl1 short. Measurements in Table 1.

Distribution.—Known only from type locality.

Biological notes.—The material, 15♂ 13♀12imm, was collected with pit-fall traps in primary evergreen rain forest by Dr. M. Verhaagh, during the period from May 1984–May 1985. See Römbke & Verhaagh (1992) for more details on type locality. No seasonal differences were observed in the occurrence of adults versus immatures and nor in males versus females. The male/female ratio was approximately equal.

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Figures 1–4.—*A-us x-us,* male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us,* holotype male; 33, 34, *A-us y-us,* male. Scale = 1.0 mm.

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